

AMERICAN JOURNAL OF BOTANY

VOL. VII

APRIL, 1920

No. 4

EMBRYO DEVELOPMENT AND POLYEMBRYONY IN RELATION TO THE PHYLOGENY OF CONIFERS¹

JOHN T. BUCHHOLZ

A consideration of embryogeny has played an important part in nearly all discussions of phylogeny, but the embryo development of conifers has offered so many variations and apparent anomalies that many students of Gymnosperms have been in doubt as to whether the embryogeny should be considered very seriously in connection with a study of the morphology of this group. So far as I know, the question of polyembryony has not generally entered into these comparisons, but has been looked upon as an extremely variable feature and one of little morphological importance. The present discussion is an attempt to take into account both the embryo development and polyembryony in making comparisons between the embryogenies of conifers, and aims to point out how these features of embryo development may prove to be very valuable criteria in arriving at the true phylogeny of the Coniferales.

Since my new interpretation of the embryogeny of conifers involves an accurate knowledge of the condition known as polyembryony, it will be necessary to consider briefly the events of proembryonic development that lead up to and accompany this condition. We will use *Pinus* as our first illustration, because its better known details of development serve as an excellent standard of comparison for the other conifers. I expect to show, further, that the embryogeny of *Pinus* occupies a very primitive position in relation to all conifers whose embryogeny has thus far been described.

PINUS

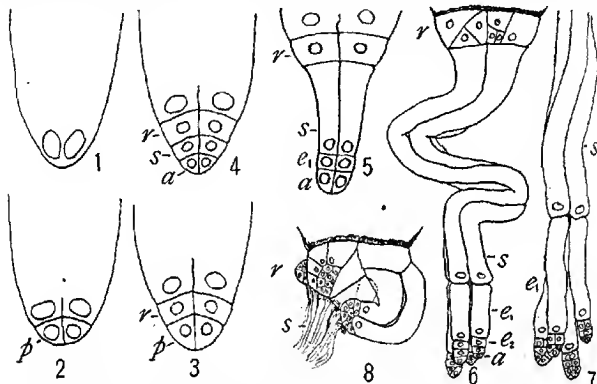
In the proembryo stage of *Pinus* it is well known that walls appear following the mitosis between the four- and the eight-nucleate stages, but it should perhaps be emphasized that after these first walls are formed (fig. 2), the cells of the lowest tier (*p*) are the initial cells which give rise to the four distinct embryos that completely separate from each other. Another free nuclear division occurs in the tier of incompletely walled cells above

¹ Invitation address read before the joint session of Section G, A. A. S., the Botanical Society of America, and the American Phytopathological Society, in the symposium on the "Phylogeny of Seed Plants," at St. Louis, December 30, 1919.

[The Journal for March (7: 83-124) was issued April 17, 1920.]

this, and hence the tier of cells *r* (fig. 3), the rosette tier, is also organized directly after a free nuclear division in the proembryo. These rosette cells are now known to be embryo initials (2).

In this stage, shown in figure 3, with the upper aborting tier of four free nuclei and with eight-walled cells beneath them arranged in two tiers, we have the initial cells of all the embryos that are regularly produced



FIGS. 1-8. Embryogeny of *Pinus*. FIGS. 1-4. Sectional views of proembryonic stages. FIG. 5. Embryos when suspensors begin elongating. FIG. 6. Separation of four embryos coming from *p*. Embryos arising from rosette (*r*) are shown in figure 8. *a*, apical cell; *s*, suspensor; *e1*, *e2*, embryonal tubes that add to suspensor; *p*, tier of initial cells of primary embryos; *r*, rosette tier.

from a single fertilized egg in the pine. Of course, some of these initials especially those of the rosette group, may abort in this stage or in any subsequent stage of development.

The embryos that arise from each of these initial cells begin their development by true apical cell growth; first the apical cell has only one cutting face, and later, when the embryos have separated, it has three cutting faces. The apical cell vanishes, usually before an embryo of more than 500 cells is formed.

Following the organization of these eight-walled cells, the embryo initials of the tier *p* undergo simultaneous division in which the tier *s* is formed (fig. 4). These first segments (*s*) of their respective apical cells elongate to form suspensor cells (figs. 5, 6), while the apical cells (*a*) form additional segments, *e1*, *e2*, etc., that elongate and add to the suspensor.

By this time the four vertical rows of cells, representing as many embryos, have separated, and the rosette cells (*r*) begin to proliferate to form the rosette embryos. The four rosette embryos usually do not actually

separate (fig. 8), but are nevertheless entirely independent of each other in their further development, while the four primary embryos completely separate from each other, eight embryos being the normal product of each egg in *Pinus*.²

CLEAVAGE POLYEMBRYONY

This separation of the zygote into a number of smaller units which undergo competition with each other is called cleavage polyembryony, to distinguish it from the simple polyembryony that may result from the fertilization of several eggs. The free nuclear divisions occurring during the proembryo stage in *Pinus* are followed by the equal cleavages which organize the initial cells of each of the embryos that separate. It is well known that only one of these many embryos, produced either by cleavage polyembryony or by simple polyembryony survives to the maturity of the seed. This is surely a "survival of the fittest" if vigor in the embryo is any sort of measure of future fitness.

This cleavage polyembryony with very definite proembryonic organization, which is present in *Pinus*, is apparently a primitive character in the development of this group of seed plants. This character tends to be modified or eliminated, reverting to the condition of simple polyembryony, as we advance along several phylogenetic lines, and is lost by the time the level of the Angiosperms is reached. If a splitting of the embryo is found among Angiosperms, which is rare, it is a cenogenetic character, a condition which has not necessarily been carried over from Gymnosperms.

It is well known that the term polyembryony when applied to Angiosperms has no such definite meaning as when applied to Gymnosperms, for among conifers the term has been used to designate the plurality of embryos which arise from the cleavage of one egg (cleavage polyembryony), or from the fertilization of several eggs (simple polyembryony), but not otherwise. Among Angiosperms, as summarized by Coulter and Chamberlain (12), the embryos are known to arise from a plurality of eggs in only two species (widely separated in phylogeny), occasionally by a process of budding from the suspensor, and in only one species by the splitting of an embryo derived from the single egg. Furthermore, the extra embryos are derived from synergids in about twelve species, from nucellar or other tissue outside of the embryo sac in eleven or more species, from antipodal cells and even from endosperm in others, while false polyembryony may occur through the fusion of ovules, etc. Clearly this Angiosperm polyembryony has little in common with the phenomenon when found in Gymnosperms.

In all Gymnosperms, polyembryony results in a selection of a single embryo from a larger number, long before the seed is matured, while in Angiosperms it is a common thing to find that several embryos survive to the maturity of the seed. The suspensor of the Gymnosperm embryo

² A more detailed review and discussion of the proembryonic development of Abietineae is given in another paper by the author (4).

is an organ of competition, the structure upon whose merit the selection of the surviving embryo depends, while in Angiosperms it is usually a chain of comparatively unelongated cells which carries the embryo into the central portion of a very soft endosperm. Ginkgo, which has a relatively short suspensor, seems to be about the only Gymnosperm which occasionally matures more than one of its several embryos, and even here Cook (11) found this occurring in only two percent of the seeds. It is much more infrequent than this in Pinus, and probably in all other Gymnosperms. It is clear that the erratic character of polyembryony in Angiosperms should not influence our judgment in deciding on the phylogenetic value of this feature in Gymnosperms.

Simple polyembryony is found among cycads, since these have constantly several archegonia; but none of them are known to possess cleavage polyembryony with its accompanying phenomena, so that polyembryony is a feature too uniform to be of value in showing the affinities of the genera within the Cycadales. However, the ordinary anatomical characters of the procumbent have been used very effectively for this purpose by Chamberlain (6).

Among conifers, much more precise comparisons of embryonic development are possible when we once understand these greater variations of the proembryo and of the early embryo brought about by cleavage polyembryony; stages of development which one would otherwise expect to find rather conservative and uniform. The peculiar splitting of the embryo, which was introduced somewhere in the ancestry of Pinus, has persisted for some time in the evolution of the conifers, and was suppressed or eliminated by a number of distinct methods. The rosette embryos, rosette cells that abort, and many other early embryo features are only results of cleavage polyembryony. Together with the apical cell (doubtless a Pteridophyte character which has persisted), these features give us a splendid array of consistent characters to serve as an index to the natural classification of the groups.

ABIETINEAE

In a very recent paper on "Polyembryony among Abietineae" (4), I have made a number of comparisons of the embryos of this group, which are summarized with greater accuracy in the diagram of figure 9. While the proembryos of all Abietineae (with the possible exception of *Pseudotsuga*) appear to be identical (4), the condition of cleavage polyembryony (*Cl.p*) is restricted to Pinus, Cedrus, and Tsuga. *Abies balsamea* displays an occasional embryo with cleavage polyembryony, but normally it has only simple polyembryony and is similar to Larix, Picea, and *Pseudotsuga* in this respect.

It will be seen that the apical cell (4) has the same range of distribution within this group. Fusion of embryos seems to be the method by which

ough of these characters disappeared from the ontogeny of the higher Abietineae.

Rosette embryos (*R-em*) usually develop in *Pinus*, are somewhat less developed in *Cedrus*, while *Abies* has rosette embryos only rarely, about

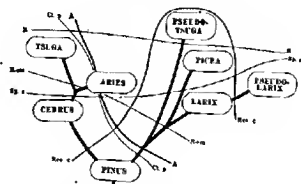


FIG. 9. Diagram to show the affinities of the genera of Abietineae, based on embryology. *A*, probable range of apical cell; *Cl.p*, range of cleavage polyembryony; *R-em*, range of rosette cells which may give rise to rosette embryos; *R*, range of abortive rosette cells. Two anatomical characters are included: *Res.c*, the range of resin canals in secondary wood, defining the Pinace of Jeffrey (19, 20); *Sp.s*, range of spur shoot, used by Engler and Gilg (16) and others in subdividing the Abietineae.

as often as it has cleavage polyembryony. However, these two occasional characters of *Abies* are not necessarily associated with each other in their occurrence.

In *Picea*, *Larix*, and *Abies balsamea* (normally) the rosette embryos are represented only by their initial cells (*R*). *Tsuga* also has only these abortive rosette cells, though its primary embryos separate as in *Pinus*. These abortive rosette cells are the last rudimentary structures that remain to indicate the origin of these embryos with simple polyembryony from the type of cleavage polyembryony found in *Pinus*.

One of the most formidable obstacles to the opposite interpretation, namely, that the embryo of the *Picea* or *Larix* type has given rise to the pine type with its cleavage polyembryony, comes from the study of these rosette cells. It is impossible for these abortive structures as represented in *Picea* or *Larix* to have given rise to the active rosette embryos of *Pinus* and *Cedrus*. On the other hand, the view that rosette embryos and the abortive rosette cells are steps in the elimination of cleavage polyembryony offers a very satisfactory hypothesis that is consistent with the facts and that very definitely points out the direction of this polyembryonous evolution.

In *Pseudolarix* the rosette cells are present (29), but nothing has been described or figured to indicate whether cleavage polyembryony or rosette embryos develop at a later stage. The exact position of *Pseudolarix* is still doubtful, but from what is known of its embryo, and considering that it resembles *Larix* in its spur shoot, it is safest to place it in the diagram near *Larix*.

In *Pseudotsuga*, the uppermost walled cells of the proembryo elongate to form the suspensor, and therefore no aborting rosette cells are found.

It is interesting to note how these embryo characters relate themselves to the results of the anatomists. The distribution of the resin canal characters described by Jeffrey (19, 20) are included in the diagram (*Res.*), cutting *Pinus* off from *Cedrus*, although these two genera are very similar on the basis of embryogeny and also in the spur shoot characters used by Engler and Gilg (16) and others as a basis for subdividing the *Abietineae*. On the other hand, the distribution of the apical cell, cleavage polyembryony, and rosette embryos cuts *Pinus* off from the rest of the *Pinaceae* of Jeffrey. The intermediate position of *Cedrus* between *Pinus* and *Abies* was pointed out by Jeffrey (19) and by Chrysler (7) on the basis of medullary rays. *Pinus* has such an array of primitive features, both embryological and anatomical, that there can no longer be much doubt of its primitive position in any natural phylogeny of *Abietineae*.

OTHER CONIFERALES.

In the light of the foregoing, let us now consider the affinities of the other *Coniferales* as revealed by their embryo development, where this is sufficiently known. The interpretations which I shall give, while not generally those given by the investigators to whom the particular work is credited, do no violence to the facts as they have been described, and for any errors due to these interpretations I assume full responsibility.

I will first present the line of evolution between *Pinus* and *Araucaria*, based on embryogeny. There are not many known types that fit in between these two very different methods of embryo development, but we have steps enough to give us a definite clue to the possible lines of advance, and to suggest the kind of embryogeny from which that of the *araucarians* was derived.

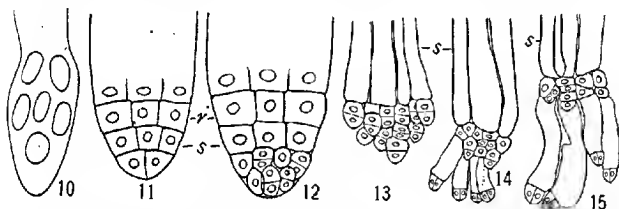
The number of free nuclear divisions is increased and a larger number of embryo initials is formed, resulting for a time in greater cleavage polyembryony. Advancing a little further, we find that only a small portion of these potential embryo initials function. Cleavage polyembryony is then eliminated by the modification of the terminal portion, which organizes a cap and prevents the embryos from splitting apart. The apical cell also persists for a time in this line of evolution, and it appears that the formation of this cap over the advancing end of the embryo is the thing which does away with the apical cell stage. Here again we have probably had the apical cell stage and cleavage polyembryony eliminated by the same device.

Even if we take the position that *Pinus* did not directly give rise to *araucarians*, it is apparent that they had a common origin and were derived from a condition of cleavage polyembryony. *Pinus* has remained in this condition with very little modification, while the *araucarian* embryogeny has become specialized, and has completely eliminated cleavage polyembry-

A few stages in this araucarian line of evolution may be illustrated by *Sciadopitys* and the podocarps.

SCIADOPITYS

The embryogeny of *Sciadopitys* (figs. 10-15) has been partially described by Lawson (27) and Arnoldi (1), and represents a step in the direction of *Araucaria*. There are at least eight free nuclei before walls form (see fig. 10), and Lawson states that "eventually the procumbryo consists of three tiers of cells and one tier of free nuclei," from which I have supplied fig. 11. However, the organization of embryo initials continues in the terminal tier



FIGS. 10-15. Stages in embryogeny of *Sciadopitys*. Figure 10 after Lawson (27) figures 11 and 12 supplied from description by Lawson; figures 13-15 after Arnoldi (1).

until a group of about 16 cells is formed (fig. 12). (This stage is also supplied from Lawson's description and from a study of the next stage (fig. 13) by Arnoldi.) Finally the suspensor tier elongates and thrusts the terminal group of cells into the gametophyte, a stage shown in figure 13. That the cells of this terminal group are really embryo initials, mostly advanced to the two-celled stage, is borne out by the next two figures.

It will be noted that in *Sciadopitys* a large number of embryo initials are produced, and the functional ones are organized in this instance *after* the first walls have formed in the proembryo; that is, the lowest functional group is not the first group of embryo initials to organize, as in *Pinus*, but the last. I would look upon a late organization of the functional embryo initials from previously walled cells as a more advanced condition, for this occurs quite generally in the more recent conifers.

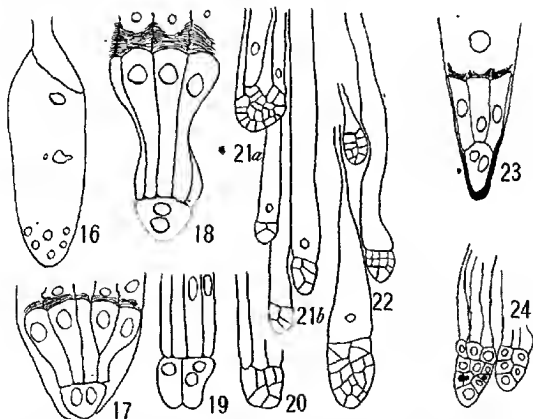
Rosette embryos undoubtedly exist in *Sciadopitys*, as Lawson accounts for walled cells above the suspensor, and Arnoldi definitely described a group of proliferating cells occupying this position which he noted as a possible vestigial protocorm, comparable to the protocorm of lycopods. He states: "Ich kann, gewiss nicht bestimmt entscheiden, ob es ein morphologisches Gebilde ist, oder eine Anpassung zur noch weiteren Polyembryonie." Unfortunately Arnoldi gave us no figures of this "protocorm," but it is probably safe to infer that he saw a group of rosette embryos, and that the entire embryogeny of *Sciadopitys* represents a modification in the direction of greater cleavage polyembryony.

PODOCARPINEAE

The embryo development of the podocarps, according to the meager descriptions available, represents a condition much further removed from *Pinus*, one which is to be looked upon as modified from a form intermediate between *Sciadopitys* and the *araucarians*. In many respects, these podocarp embryos illustrate some of the general tendencies of embryo modification which brought about the highly specialized *araucarian* type, and are therefore considered here.

The proembryo of *Podocarpus* (fig. 17) consists of two very unequal tiers of cells, and some free nuclei in an open tier above. Figure 18 shows an early proembryo with suspensors elongating, and with its binucleate terminal cell undergoing further division in figure 19 before the embryo initials, which may separate, are formed. From the fact that these suspensor cells in this case were organized from free nuclei, one could infer that these are suspensor-forming embryo initials. The rosette cells of *Pinus*, which certainly are embryo initials, were sometimes found to elongate as suspensors (2), and we might expect to find some groups of conifers in which such unfavorably placed embryo initials are normally modified to form suspensors.

While *Podocarpus coriaceus* (figs. 16-22), which was investigated by Coker (8), produced walls only after sixteen or more free nuclei were formed,



FIGS. 16-24. Stages in embryogeny of *Podocarpus coriaceus*, after Coker (8). FIG. 23. *Podocarpus nivalis*, showing binucleate terminal cell enclosed by a thick cellulose cap. FIG. 24. Embryos of *P. ferrugineus*. Apical cell stage appears to exist in figures 20 and 21b-24. Figures 23 and 24 after photomicrographs by Sinnott (39).

Sinnott (39) described *P. tolara* and *P. nivale* as producing walls at an earlier stage, which fact places the Podocarpaceae a little closer to the Abietineae.

Coker states that either the embryo may split up or its parts may unite in producing the embryo, but it is highly probable that cleavage polyembryony is the normal condition in the species which he investigated. All his figures of embryos that presumably were produced by simple polyembryony appear very much like those which one would expect to see in the older separated embryos which have a secondary suspensor, and we know that all conifers produce such secondary additions to the suspensor by the elongation of cells to form embryonal tubes. From the interlocking articulation of the embryo of figure 21a with its suspensor, it is evident that these are embryonal tubes and not the primary suspensor, as inferred by Coker; but the largest embryo of this group is not the terminal one in this particular instance.

It is also possible that the apical cell stage is found in these separating embryos of Podocarpus, as may be seen by a careful study of figures 21-24. No rosette cells are found in the above described species (I refer to walled rosette cells, not the free nuclei that abort above).

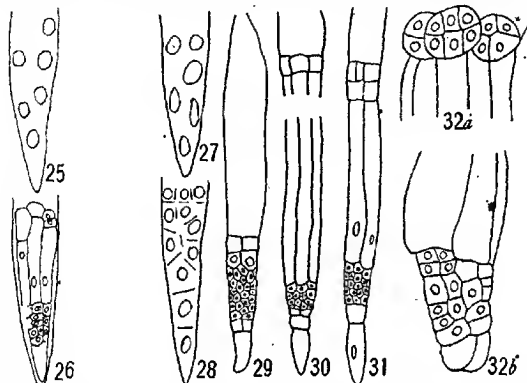
In *Podocarpus nivalis*, Sinnott described and figured a thick cellulose cap "protecting" the binucleate terminal cell, as shown in figure 23, which is pushed far into the gametophyte before it divides further, and "instances of budding or of single suspensors giving rise to embryos were only rarely observed." Does it not appear that this thick cellulose cap would tend to prevent a splitting of the embryo and so to cause the initial cells of the lower tier to combine and produce a single embryo?

I have occasionally observed a cap of wall thickening which appeared to hold together the terminal cells in the embryo of *Pseudotsuga*,³ but this structure is not found in the slightly later stages. It is evident that cleavage polyembryony occurs only with considerable difficulty where such a thick cellulose cap protects the terminal group of cells. I am inclined to look upon these caps as mechanical devices which prevent cleavage polyembryony.

Another type of embryo development, probably a higher specialization of that above described, is also found in the Podocarpaceae. I refer for illustration to the embryo of *Podocarpus spicatus* (figs. 25-26), one of the Stachycarpus group (39), in which the terminal cells organize into a cap while the cells above the cap give rise to a single embryo and its suspensor of embryonal tubes. In this case we have no cleavage polyembryony, and it appears that the function of this cap, which is soon sloughed off, may be to prevent this splitting of the embryo, a danger present only in the first stages. However, it would probably not prevent cleavage polyembryony as successfully as the more elaborate caps found in *Araucaria* and *Agathis*.

³ Unpublished work.

The *Cephalotaxus* embryo shown here in figures 28-32 doubtless has been modified from something like this *Podocarpus spicatus* type of embryo. It has, however, a feature which would relate it more directly to *Phytol*



FIGS. 25-26. Stages in embryogeny of *Podocarpus spicatus*, showing terminal cap cell, suspensor cells beginning to elongate, and the group of embryo-forming cells between. After photomicrographs by Sinnott (39). FIGS. 27-32. Stages in embryogeny of *Cephalotaxus*, showing terminal group of cap cells, embryo-forming cells, suspensor, and what is probably a group of rosette cells in 32a. FIG. 27. *C. drupacea*, after Lawson (25). FIGS. 28-32. *C. Fortunei*; figure 28 after Coker (10), and figures 29-32 after Strasburger (41).

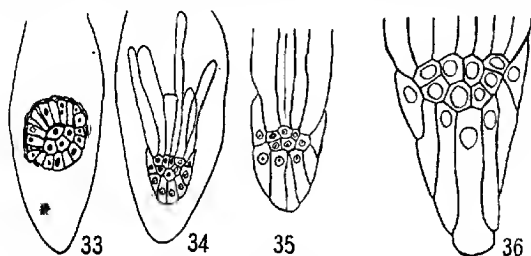
namely, a conspicuous group of rosette embryos (fig. 32a) above the suspensor. The figures here shown are taken from Strasburger (41), who delineated this feature without comment. A similar condition of the rosette may yet be found in the podocarps, for it seems to be suggested by figure 26.

The group of cap cells in this case is probably also a device to prevent cleavage of polyembryony or apical cell growth, for this cap is also sloughed off (fig. 32b) soon after the proembryo stage, the stage in which cleavage polyembryony is found, if at all.

ARAUCARINEAE

While I would not derive the araucarian type of embryo with its elaborate cap (figs. 33-36) from these podocarp embryos, it is probable that these two groups had a common origin, that the caps of the embryos of both were derived in response to similar conditions, and that these peculiar structures in both instances serve to prevent cleavage polyembryony. The increase in the number of free nuclear divisions in the proembryos of both these groups may be due to a past history of greater cleavage polyembryony, which might well have been overcome by a mechanical device.

In the Podocarpaceae and Cephalotaxus, the functional initials were reduced by the abortion of a large portion of the free nuclei in the proembryo, the walled cells below these became suspensor-like, and cleavage poly-



FIGS. 33-35. Stages in embryogeny of *Agathis australis*. FIG. 33. Proembryo after wall formation, $\times 200$. FIG. 34. After cap is formed and suspensor begins to elongate, but before archegonium is filled, $\times 260$. FIG. 35. Section through tip of older embryo showing the small cells below the suspensor from which the embryo is derived, $\times 460$. After photomicrographs by Eames (15). FIG. 36. Embryo of *Araucaria brasiliensis*, drawn to half the scale of figure 35, $\times 230$. After photomicrograph by Burlingame (5).

embryony was eliminated by the organization of caps of various kinds; while in the Araucarineae all the free nuclei are utilized and become organized into an embryo whose terminal portion has a multicellular cap, as shown in figures 33-36.

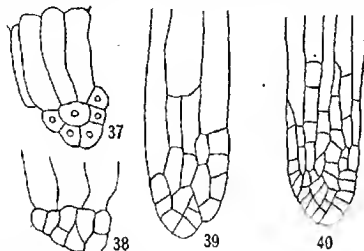
These embryos of *Agathis* and *Araucaria* were very satisfactorily described by Eames (15) and Burlingame (5), and neither of these investigators found cleavage polyembryony. In both these species the free nuclear divisions of the proembryo are essentially the same. The proembryo is confined to a small portion of the egg cytoplasm, and the embryo has begun to elongate considerably before the archegonium is filled by its tissue. The entire embryogeny of the Araucarineae bespeaks a high degree of specialization.

That the cap is not particularly useful in protecting the embryo in its penetration of the gametophytic tissue was brought out by Burlingame (5), and the possibility that it is a special secretory organ is just as remote; but, since other conifers appear to have developed mechanical devices to prevent cleavage polyembryony, an explanation of this nature is possible.

An explanation which would derive the Abietineae from the Araucarineae on the basis of embryogeny is beset with great difficulty, if not impossible; but it is not so difficult to show how the araucarian embryo has developed from a form very similar to that of *Pinus* as a specialization along a particular line. At the same time this latter theory offers a satisfactory explanation for the nature of the cap.

TAXADS

The taxad line may have been derived from some of the podocarps, or more probably along with these from a condition nearer to that of *Pinus*. In *Taxus* (18) there are at least 16 free nuclei before walls form, and the terminal tier of the proembryo may contain several cells, probably all of



FIGS. 37-40. Stages in embryogeny of *Taxus baccata*, $\times 125$. FIG. 37. Proembryo at beginning of suspensor elongation, after Hofmeister (17). FIG. 38. Slightly later stage. FIGS. 39 and 40. Later stages showing apical cell in early embryo. Figures 38-40, after Strasburger (40).

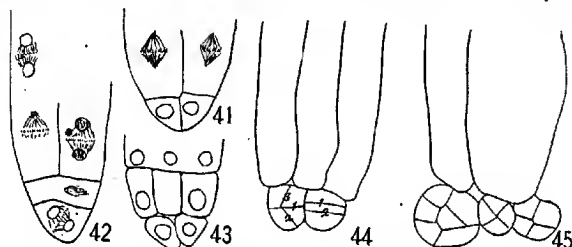
them potential embryo initials. Apparently one of these several cells, doubtless the one most favorably situated, begins to cut off apical cell segments and gains the ascendancy over the others (40), which in turn contribute by their activity to the suspensor. Figures 39-40 by Strasburger (40) show that the apical cell persists for some time, and this furnishes an instance of the elimination of cleavage polyembryony with the retention of the apical cell.

According to Jäger (18), some of the upper suspensor cells of *Taxus* may occasionally break away and appear to give rise to small secondary embryos, but practically always the proembryonic cells all combine into a single embryo. Thus, *Taxus baccata* appears to have practically overcome cleavage polyembryony, but still shows some vestigial evidence of an origin from this condition. In commenting on this Jäger (page 182) makes the significant statement that it appears to him that occasionally all the cells of the early proembryo show a capacity for giving rise to embryos, and in this statement he seems to have approached very close to the present explanation.

In *Torreya*, the proembryonic tissue fills the entire egg, while in *Taxus* it is confined to the lower portion of the egg. *Torreya* has only four free nuclei before walls form, and, though no cleavage polyembryony occurs, the vestigial evidence of it in the form of occasional secondary embryos has been described (14). The differences between *Taxus* and *Torreya* may be looked upon as due to higher specialization of the latter, and it is therefore questionable if the apical cell stage exists in *Torreya*.

TAXODINEAE

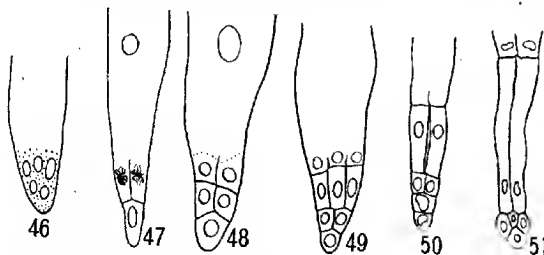
Among Taxodineae, the excessive cleavage polyembryony described for *Seladropitys* becomes reduced, as illustrated by *Taxodium* (9) (figs. 41-45). Figure 43 doubtless represents two unequal tiers of embryo initials in addition to the upper aborting nuclei. The lowest tier forms separate embryos (fig. 44), while the next tier of initials above it forms suspensor



FIGS. 41-45. Stages in embryogeny of *Taxodium distichum*, $\times 200$. After Coker (9).

cells. Cleavage polyembryony is apparent. It is probably the normal condition, and we sometimes have the organization of embryo initials after the first appearance of walls, as shown in figure 42. Coker shows the order in which the walls appear in the embryos of figure 44, which is a good start for an apical cell stage. In general the embryo of *Taxodium* shows great similarity to that of *Pinus*, except for the unequal organization of the tiers in the proembryo (see figs. 41 and 43) and the absence of the rosette cells.

Cunninghamia (28) may be a step higher, for here it is highly probable (judging from the few stages described by Miyake (figs. 46-51)) that only the lowest embryo initial gives rise to the embryo. This may have been the method of overcoming cleavage polyembryony in this line of evolution,



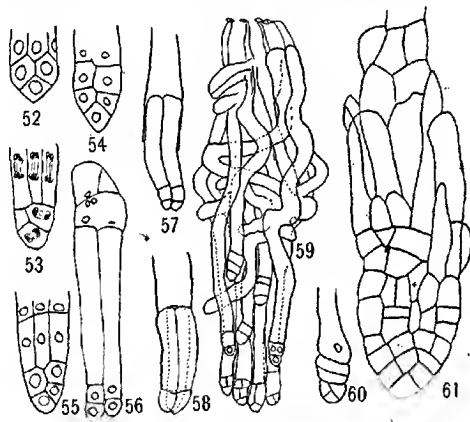
FIGS. 46-51. Stages in embryogeny of *Cunninghamia sinensis*, $\times 110$. After Miyake (28).

the functioning of only the lowest embryo initial, the others giving rise to the suspensor. Whether or not an apical cell organizes in *Cunninghamia* remains to be discovered.

Cryptomeria (24) belongs somewhere in this group on the basis of embryogeny, but the account and figures given by Lawson are not complete enough to warrant any definite conclusions.

CUPRESSINEAE

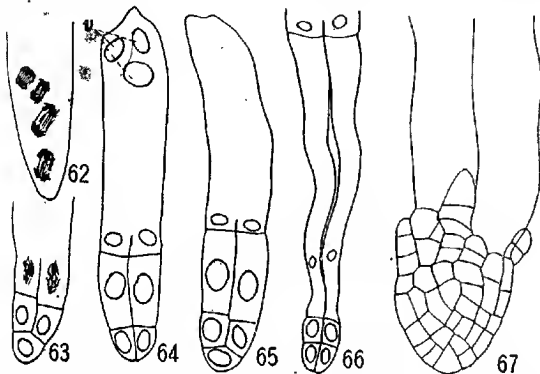
In the Cupressineae, the proembryo also resembles that of *Pinus* except for the unequal tier organization. In *Juniperus* (figs. 52-61), which represents the condition nearest to *Pinus*, the proembryo seems to organize



FIGS. 52-61. Stages in embryogeny of *Juniperus*. FIGS. 53 and 55. *Juniperus communis* var. *depressa*, $\times 150$, after Nichols (30). FIGS. 52, 54 and 56. *J. communis*, after Noren (31). FIG. 58. Same, after Hofmeister (17). FIGS. 57, 59-61. *J. virginiana*, after Strasburger (40). Figure 59 shows the many embryos arising from an archegonial complex, multiplied further by cleavage polyembryony, $\times 75$. FIGURES 56-58 indicate that an uneven tier arrangement (shown in figures 52 and 54) is no hindrance to cleavage embryony. Figure 53 shows that embryo initials may organize after the first walls form, and figures 60 and 61 ($\times 185$) show the apical cell.

with the usual embryo initials in several tiers and, above, some inactive nuclei that abort (17, 30, 31, 40). The walled cells below these aborting nuclei function as suspensors, while the lowest group of embryo initials becomes organized into embryos that separate. FIGURES 56-59 show that cleavage polyembryony is found, and figures 59-61 that the apical cell stage is probably the normal condition.

Thuja (figs. 62-67) is a step higher, for here cleavage polyembryony does not occur normally. I find from my own studies¹ of this species that it occurs occasionally, probably coming from such embryos as shown in figures 64 and 66 by Land (21). In most cases, one of the embryo initials,



FIGS. 62-67. Stages in embryogeny of *Thuja occidentalis*. Figures 62-66, after Land (21), $\times 300$. FIG. 67. Later stage showing apical cell of embryo, $\times 225$, after Strasburger (40).

such as the lowest of figure 65, has a more favorable position and gives rise to the embryos, the others only elongating to form the suspensors.

Whether only the terminal embryo initial functions or several of them, an apical cell stage is always found; a very conspicuous feature in *Thuja* (fig. 67). From my own studies¹ of *Thuja occidentalis*, I can also state that rosette embryos are found in a significant number of cases, but they are not found in *Thuja orientalis*.

Tetraclinis probably represents a more advanced condition than *Thuja*, for it appears that only the terminal embryo initial functions. Saxton (36) reported no splitting embryos, but found that several tiers of the proembryo may contribute to the suspensor. However, the existence of cleavage polyembryony may easily have been overlooked.

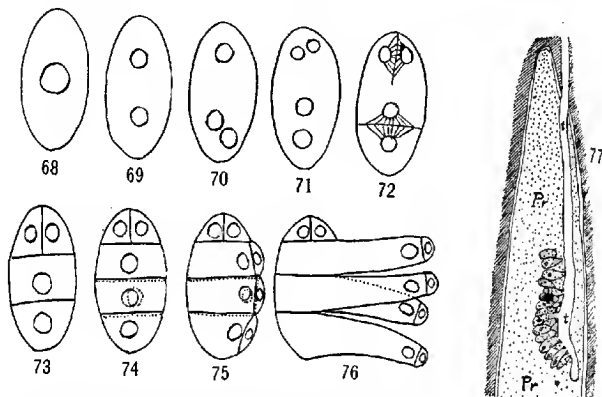
In *Libocedrus*, which was studied by Lawson (26), the embryogeny is also too little known to justify any conclusions, and the embryogeny of both *Tetraclinis* and *Libocedrus* should be reinvestigated to clarify some of these points.

The *Taxodineae* and *Cupressineae* appear to be very similar on the basis of embryogeny, both groups showing an evolution from cleavage polyembryony to simple polyembryony, but our knowledge of both of these groups is at present very unsatisfactory.

¹ Unpublished work.

ACTINOSTROBUS AND CALLITRIS

The *Actinostrobus* and *Callitris* type of embryo development (figs. 68-76) has certainly been derived from one of the types already described, probably from that of the *Cupressineae*. In *Actinostrobus* (35), the first walls appear earlier, between the two- and the four-nucleate stages. The proembryo tissue fills the entire egg, and the separate embryo initials are not organized from the first walled cells, as in *Pinus*, but after one of the



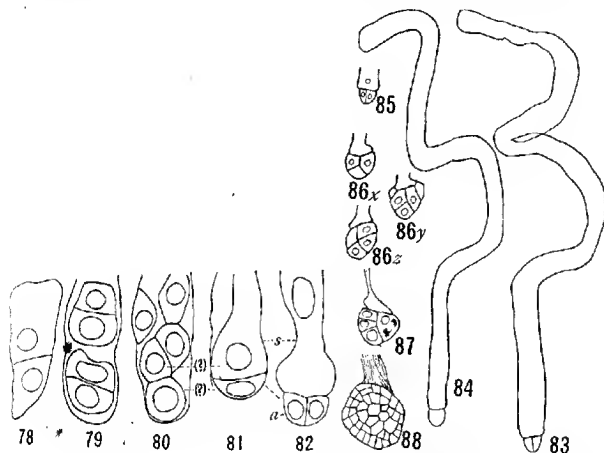
FIGS. 68-76. Diagrams to represent proembryo of *Actinostrobus*. *Callitris*, and probably *Widderingtonia*, are very similar. After Saxton (35). FIG. 77. Gametophytes of *Callitris*, showing large lateral archegonial complex, in its relation to the pollen tube (Pt.). After Saxton (34).

succeeding divisions. Two of the first walled cells undergo no further development, and four embryo initials are organized in the remainder of the egg. Figure 77 shows the relation of the gametophytes and the lateral archegonial complex in *Callitris*. From this it will be seen that the embryos which grow out laterally from these archegonia penetrate the gametophyte in the usual manner. Saxton, to whom we are indebted for our knowledge of this interesting embryogeny, states that *Callitris* (34) is very similar, while *Widderingtonia* (32, 33) is transitional between this and some of the *Cupressineae*. Cleavage polyembryony is a constant feature, and in all probability the apical cell is also found in the first stages of the embryo.

Widderingtonia, *Actinostrobus*, and *Callitris* have been placed in a separate sub-family, the *Callitroideae*, by Saxton (37), largely on the basis of the gametophytic and embryonic characters, and it seems that there is good ground for including these in a group distinct from the other *Cupressineae*.

SEQUOIA

In the proembryo of *Sequoia* (23) the tendency to an early wall formation is carried a step further than in the forms previously described, for a wall is laid down after the first division of the egg nucleus (fig. 77). Each of these proembryo cells rounds off more or less, and the cells resulting from



FIGS. 78-82. Stages in the embryogeny of *Sequoia sempervirens*, $\times 250$, after Lawson (23).

FIGS. 83-88. Later stages in the embryogeny of *Sequoia*, after Arnoldi (1); figure 87 showing an apical cell. FIGS. 86x, y, z, series of three sections through an eight-celled embryo showing apical cell, after Shaw (38).

the next division are similarly dissociated. According to my interpretation, these cells shown in figures 79 and 80 are separately organized embryo initials, all but the lowest of which abort; at least their further development has not been observed. The lowest cell of figure 79 (or the lowest of figure 80, a point not made clear in the account by Lawson) gives rise to the embryo shown in the succeeding figures, the suspensor cell being the first cell cut off from the embryo initial. This earlier wall formation, the proembryonic tissue filling the entire egg, and the suppression of cleavage polyembryony by the abortion of embryo initials, are some of the advanced embryo characters illustrated by *Sequoia*.

There is probably at least a short apical cell stage in *Sequoia*, according to the figures of Shaw (38) and Arnoldi (1), shown here in figures 83-88.

EPHEDRA

I cannot refrain from including a mention of the Gnetales in this discussion, for these have polyembryony, much as have the Coniferales. In the embryo of Ephedra (22, 40), for example, cleavage polyembryony is the regular occurrence. The free nuclei which are concerned in the organization of the embryo initials do not all descend to the bottom of the egg, as in Pinus, but remain in comparative independence of each other, and this condition of cleavage polyembryony is very striking. Judging from the published accounts and figures there is not much probability that an apical cell stage is to be found, and this would furnish us an instance in which the apical cell is eliminated and cleavage polyembryony is retained. It seems to me that this feature of cleavage polyembryony very definitely marks the Gnetales as having been derived from the conifers rather than from the cycads.

There is perhaps no better way for me to summarize these many comparisons of embryo development made during the course of this discussion, than to use the method of a diagram, as was done for the Abietineae. Such a scheme of phylogeny represents only the present status of our knowledge concerning embryogeny and is not intended to be accurate to the last details, for many of these details have been too inadequately described. It doubtless represents fairly accurately the affinities of the larger groups.

In this diagram (fig. 89), the ranges of the various embryonic features which have been discussed are plotted in light lines, while the (probable) phylogenetic connections suggested by embryogeny are shown in the heavy lines. The range of the apical cell (*A*), and cleavage polyembryony (*Cl.p*) are marked with some uncertainties, but in general it appears that the latter is more limited in its range than is the apical cell. The archegonial complex is found in all forms surrounded by the circle *Cx*. Rosette embryos are not plotted, but the forms having rosette cells are marked as follows: *R*, rosette cells; (*R*), occasional rosette cells; *R-em*, rosette cells that develop embryos; *R-(em)*, rosette cells that occasionally give rise to embryos, etc. The rosette embryos are therefore also primitive features that soon vanish, followed by the disappearance of the rosette cells, which are the last vestiges of cleavage polyembryony. The embryo cap (*Emb.cap*) found in *Araucaria* and *Agathis* is an advanced feature found also in the forms somewhat involved in the evolution of the Araucarineae.

It will be found that in general the cotyledon number decreases as we proceed upward in every direction away from Pinus. Though the number of cotyledons is somewhat variable throughout, this number is reduced sooner or later among conifers (3) to the limit of three or two.

I have included the range of one well-known taxonomic feature in this diagram, namely, the spur shoot (*Sp.S*). *Sciadopitys* with its double needles

in the axil of a bract has doubtless also the morphological equivalent of the spur shoot. If the phylloclad, which occupies the same position on the stem, could be looked upon as the morphological equivalent of this dwarf branch, we should have the dimorphic branches represented in a

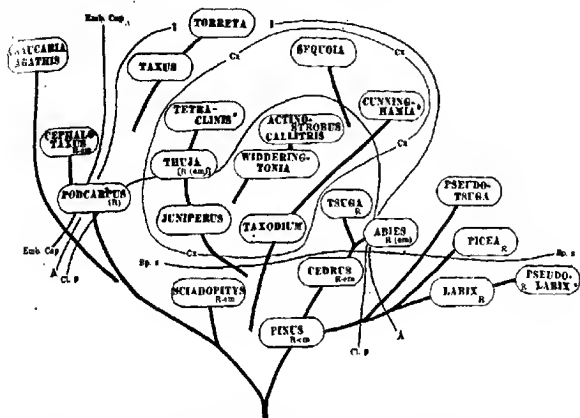


FIG. 29. Diagram representing the affinities of the Coniferales as suggested by embryogeny. *A*, probable range of distribution of apical cell in early embryo; *Cl. p.*, probable range of cleavage polyembryony; *Emb. cap.*, range of distribution of embryo cap; *Cx*, distribution of archegonial complex; *R*, rosette cells present; *R-em*, rosette cells that usually give rise to rosette embryos; *R-(em)*, rosette cells and rosette embryos occasional only; *Sp. s.*, range of distribution of spur shoot. Position of forms marked with asterisk (*) is doubtful.

member of the Podocarpaceae. Jeffrey (20) looks upon the spur shoot as a primitive feature, and it would appear at least that this dwarf branch is a character present in the most primitive representatives of more than one line of evolution.

Unfortunately the embryogeny of a large number of conifers is not known, and many forms that have been studied have been described in such a way that we are uncertain of the features with which we are most concerned in the present discussion. Enough has been described to indicate that with some such organization of the facts as here presented, embryogeny must occupy a much more important place in the study of comparative morphology than has generally been conceded.

The origin of cleavage polyembryony, a very interesting question, has not been shown in any living conifer thus far described. A theory to account for the possible origin of this condition has been formulated and is to be published at another time.

SUMMARY

This brief review has summarized, or taken into account, practically all of the published work on the embryogeny of conifers in the proembryo and early embryo stages. It is shown how the known facts may be harmonized under the conception that the Coniferales have been derived from forms with cleavage polyembryony, and that this feature tends to be more or less eliminated as we pass from the lower to the higher forms. The apical cell, cleavage polyembryony, rosette embryos, rosette cells, and the direct organization of embryo initials from the free nuclei of the proembryo, are regarded as primitive features, while the organization of embryo initials after walls form in the proembryo, a proembryo that fills the entire egg with cells, the archegonial complex, the embryo cap, and the return to simple polyembryony, must be regarded as advanced or specialized features. Transitional conditions may also be recognized, and some of the vestigial characters, in disappearing by gradual steps, make this interpretation of the direction of evolution from cleavage polyembryony back to simple polyembryony very certain. Embryogeny must occupy a much more important place in the comparative morphology of conifers than has generally been conceded.

UNIVERSITY OF ARKANSAS,
FAYETTEVILLE, ARK.

LITERATURE CITED

Additional citations on the embryogeny of Abietineae with review may be found in the writer's paper on Abietineae (4).

1. Arnoldi, W. Beiträge etc. V. Weitere Untersuchungen der Embryogenie in der Familie der Sequoiaceen. Bull. Soc. Imp. Nat. Moscou, n.s. 14: 449-476. pls. 7-8. 1900.
2. Buchholz, J. T. Suspensor and early embryo of Pinus. Bot. Gaz. 66: 185-228. pls. 6-10, figs. 3. 1918.
3. ——. Studies concerning the evolutionary status of polycotyledony. Amer. Journ. Bot. 6: 106-119. figs. 25. 1919.
4. ——. Polyembryony among Abietineae. Bot. Gaz. 69: 153-167. figs. 15. 1920.
5. Burlingame, L. L. The morphology of *Araucaria brasiliensis* III. Fertilization, the embryo, and the seed. Bot. Gaz. 59: 1-39. pls. 1-3. 1915.
6. Chamberlain, C. J. The living cycads. Chicago, 1919.
7. Chrysler, M. A. The medullary rays of Cedrus. Bot. Gaz. 59: 387-396. figs. 7. 1915.
8. Coker, W. C. Notes on the gametophytes and embryo of Podocarpus. Bot. Gaz. 33: 89-107. pls. 5-7. 1902.
9. ——. On the gametophytes and embryo of Taxodium. Bot. Gaz. 36: 1-27, 114-140. pls. 1-2. 1903.
10. ——. Fertilization and embryogeny of *Cephalotaxus Fortunei*. Bot. Gaz. 43: 1-10. pl. 1, figs. 5. 1907.
11. Cook, Mel T. Polyembryony in Ginkgo. Bot. Gaz. 36: 142. 1903.
12. Coulter, J. M., and Chamberlain, C. J. Morphology of Angiosperms. New York 1903.
13. ——. Morphology of Gymnosperms. Chicago, 1910 and 1917.
14. ——, and Land, W. J. G. Gametophytes and embryo of *Torreya taxifolia*. Bot. Gaz. 39: 161-178. pls. A, 1-3. 1905.

12. Eames, A. J. The morphology of *Agathis australis*. *Annals of Botany* 27: 1-38. pls. 1-4. 1913.
13. Engler, A., and Gilg, E. *Syllabus der Pflanzenfamilien*. Berlin, 1912.
17. Hofmeister, W. Higher cryptogamia and fructification of the Coniferae. Translation, Ray Society, London, 1862.
18. Jäger, L. Beiträge zur Kenntniss der Endosperm-bildung und zur Embryologie von *Taxus baccata*. *Flora* 86: 241-288. pls. 15-19. 1899.
19. Jeffrey, E. C. The comparative anatomy of Coniferales II. The Abietineae. *Mem. Boston Soc. Nat. Hist.* 6: 1-37. pls. 1-7. 1904.
20. —. The anatomy of woody plants. Chicago, 1917.
21. Land, W. J. G. A morphological study of Thuja. *Bot. Gaz.* 34: 249-259. pls. 6-8. 1902.
22. —. Fertilization and embryogeny in *Ephedra trifurca*. *Bot. Gaz.* 44: 273-292. pls. 20-22. 1907.
23. Lawson, A. A. The gametophyte, archegonia, fertilization, and embryo of *Sequoia sempervirens*. *Annals of Botany* 18: 1-28. pls. 1-4. 1904.
24. —. The gametophyte, fertilization and embryo of *Cryptomeria japonica*. *Annals of Botany* 18: 417-444. pls. 27-30. 1904.
25. —. The gametophytes, fertilization, and embryo of *Cephalotaxus drupacea*. *Annals of Botany* 21: 1-23. pls. 1-4. 1907.
26. —. The gametophytes and embryo of the Cupressineae with special reference to *Libocedrus decurrens*. *Annals of Botany* 21: 281-301. pls. 24-26. 1907.
27. —. The gametophytes and embryo of *Sciadopitys verticillata*. *Annals of Botany* 24: 403-421. pls. 29-31. 1910.
28. Miyake, K. The development of the gametophytes and embryogeny of *Cunninghamia sinensis*. *Beih. Bot. Centralbl.* 27: 1-25. pls. 1-5, figs. 2. 1910.
29. —, and Yasui, K. On the gametophytes and embryo of *Pseudolarix*. *Annals of Botany* 25: 639-647. pl. 48. 1911.
30. Nichols, G. E. A morphological study of *Juniperus communis* var. *depressa*. *Beih. Bot. Centralbl.* 25: 201-241. pls. 8-17, figs. 4. 1910.
31. Noren, C. O. Zur Entwicklungsgeschichte des *Juniperus communis*. *Uppsala Universitets Arsskrift* 1907. pp. 64. pls. 4.
32. Saxton, W. T. Preliminary account of the development of the ovule, gametophytes, and embryo of *Widderingtonia cupressoides* Endl. *Bot. Gaz.* 48: 161-178. pl. 11, figs. 3. 1909.
33. —. Contributions to the life history of *Widderingtonia cupressoides*. *Bot. Gaz.* 50: 30-48. pls. 1-3. 1910.
34. —. Contributions to the life history of *Callitris*. *Annals of Botany* 24: 557-569. pls. 45, 46. 1910.
35. —. Contributions to the life history of *Actinostrobus pyramidalis*, Miq. *Annals of Botany* 27: 321-345. pls. 25-28. 1913.
36. —. Contributions to the life history of *Tetradlinis articulata* Masters, with some notes on the phylogeny of the Cupressineae and Callitroideae. *Annals of Botany* 27: 577-603. pls. 44-46, figs. 9. 1913.
37. —. The classification of conifers. *New Phytologist* 12: 242-262. fig. 1. 1913.
38. Shaw, W. R. Contribution to the life history of *Sequoia*. *Bot. Gaz.* 21: 332-339. pl. 24. 1896.
39. Sinnott, E. W. The morphology of the reproductive structures of the Podocarpaceae. *Annals of Botany* 27: 39-82. pls. 5-9, figs. 9. 1913.
40. Strasburger, E. Die Coniferen und die Gnetaceen. Jena, 1872.
41. —. Die Angiospermen und die Gymnospermen. Jena, 1897.

THE LIVING CYCADS AND THE PHYLOGENY OF SEED PLANTS¹

CHARLES J. CHAMBERLAIN

Phylogeny is a big word and it can be made to cover most of the problems of relationship. Among the phylogenetic problems of a group, two always stand out prominently: "What has been its origin?" and "Has it left any progeny?"

In the cycads these two problems are not equally difficult, for the origin can be traced back, with more or less certainty, to the ferns; but whether they have left any progeny is doubtful. However, if we stick close to the living cycads, it seems safe to claim that none of the nine genera has left any progeny or is likely to have any descendants. Like the higher members of the Cycadofilicales and Bennettitales, they are the last of their race; and if there should be another epoch succeeding the present, just as the present succeeded the Mesozoic, the Cycadales would become extinct, just as the Bennettitales became extinct.

First let us consider the less difficult problem, the origin of the cycads.

Just how far back the cycads extend, is a question which could be answered only by complete geological evidence; but what we know of available structures shows that the line goes back farther than any fossils yet discovered would indicate.

A morphologist must depend largely upon comparative morphology in studying relationships, tracing each structure, geologically, from its earliest appearance, and tracing the ontogeny wherever material is available.

The graphic method will illustrate clearly some of the principal features in the comparative morphology of cycads and at the same time will indicate their geological distribution (Plate VI).

A very prevalent fern habit—a crown of pinnate leaves at the top of an unbranched stem—has been retained by the cycad line, with remarkable tenacity, from their earliest appearance up to the living forms. The armor of persistent leaf bases is another character which can be traced from the Paleozoic up to the living forms. The large pith, comparatively scanty zone of wood, and large cortex are features common to the living cycads, Bennettitales, and Cycadofilicales (Plate VI).

If these three features—the crown of pinnate leaves, the unbranched stem with its armor of leaf bases, and the topography of a transverse section of the stem—were the only features worth considering, there could be little

¹ Invitation address read before the joint session of Section G, A. A. S., the Botanical Society of America, and the American Phytopathological Society, in the symposium on the "Phylogeny of Seed Plants," at St. Louis, December 30, 1919.

of action to putting the entire Cycadophyte phylum into one family. But when one turns to the reproductive structures, it is evident that the ancestral stock, the Cycadofilicales, has either differentiated into two lines, or has given rise to the Bennettitales, which, very soon, gave rise to the Cycadales.

The spore-bearing structures of the Cycadofilicales may be represented diagrammatically: In the center, a crown of much reduced leaves, bearing seeds; just outside these, a crown of reduced leaves—but not so much reduced—bearing microsporangia. But in none of the Paleozoic forms, the Cycadofilicales, is either of these two crowns of reduced spore-bearing leaves compacted into cones. This feature marks the Cycadofilicales, for in the succeeding forms one or both of these crowns of reduced leaves become compacted into cones (Plate VI).

The Bennettitales and Cycadales are best separated from each other by the fact that, in the former, the microsporophylls have not yet been compacted into cones; while in the Cycadales the microsporophylls form closely compacted cones. In both groups, the ovulate structures form cones, except in the genus *Cycas*.

The microsporophyll is easily traced, not only from the Paleozoic Cycadofilicales, but even from the ferns, up to the living cycads. It was the close resemblance of this microsporophyll to the spore-bearing leaves of Marattiaceous ferns, as well as the close resemblance in vegetative leaves, that led to the earlier geologists to call the Carboniferous "The Age of Ferns."

Throughout the series, the microsporangia are borne on the margin or on the under (abaxial) side of more or less reduced leaves. In the Bennettitales the microsporophylls, while much smaller than the foliage leaves, still show the pinnate character, with no tendency toward becoming compacted into cones. In the Cycadales, the pinnate character has been lost entirely and, in every genus, the compact cone stage has been reached. But the resemblance to a leaf is still seen in the prevailing distribution of the sori into two groups, representing the two series of pinnae, one on each side of a midrib (Plate VI).

The structure of the individual microsporangium has changed very little since the phylum was differentiated from the ferns. It would be interesting to compare the contents of pollen grains of Carboniferous, Mesozoic, and living forms; but no satisfactory fossil material has been sectioned. It seems safe to say that there were no pollen tubes in the carboniferous forms. Engler's term *Siphonogamia* would not include these early seed plants. The small size of the pollen grains, together with the absence of the pollen-tube habit, would indicate that the sperms were very small and that germination and the development of sperms took place very rapidly, as in our living heterosporous ferns.

The immense size of the sperms in the living cycads is an example of giantism which—so paleozoologists tell us—indicates that the phylum has reached its limit and is ready for extinction.

The megasporophyll of *Cycas* is of the greatest importance in tracing relationships, for it is essentially identical with the megasporophyll of the Paleozoic genus *Pecopteris*; while in the living cycads, a series of genera like *Cycas*, *Dioon*, *Macrozamia*, and *Encephalartos* shows the gradual reduction of the individual sporophyll and, at the same time, shows how a loose crown of sporophylls has been compacted into a cone (Plate VI).

This megasporophyll of *Cycas* is so different from any yet described in the Bennettitales that we think it is safe to claim that the Cycadales have not come from any forms like Cycadeoidea, or from any others with such reduced seed-bearing structures. While we should recognize the phenomenon known as atavism, or reversion, we believe it could appear only after a rather limited time. We can easily believe that a *Pecopteris*-like megasporophyll has persisted from the Paleozoic up to the present time; but we could not believe that the megasporophyll of Cycadeoidea, if reduced from a *Pecopteris* type, could—after millions of years—revert to the *Pecopteris* type, and so give rise to a megasporophyll like that of *Cycas*. We might believe in spontaneous generation and in the special creation of species, but not in that.

Consequently, if the Cycadales are a branch from the Bennettitales, the point of union is so far back that it becomes a question of arbitrary definition rather than a question of fact whether there has been a main stock with an early branch, or whether there have been simply two lines coming independently from the Cycadofilicales.

This seems to me to answer the question, "What was the origin of the living Cycads?" as far as it can be answered in the present state of our knowledge. If Professor Wieland would give us three big books on the Cycadales of the Triassic, Jurassic, and Cretaceous, like his three big books on the Bennettitales, we could state facts instead of spinning theories.

In tracing the plane body, with its stem, leaves, and spore-producing structures, from the Paleozoic up to the living cycads, the record is fairly complete, and there is not a very serious danger of mistakes; but in tracing the origin of the seed the Cycadophyte line has afforded little evidence, for the seeds—as far as they have been described—are almost as highly developed in the Paleozoic as they are today. In this line, they must have come from heterosporous ferns. But, until some one finds and sections a convincing series in heterosporous ferns, or in some more primitive members of the Cycadofilicales than any yet discovered, we must base our theories of the origin of the seed upon the behavior of living heterosporous forms which have not quite reached the seed stage.

What is the answer to the second question, "Have the Cycads left any progeny?"

Something has left some progeny; for an abundant progeny, both Angiosperm and Gymnosperm, is very visible and very much alive. What groups could have been responsible for this progeny?

If we consider only the nine genera of living cycads, as we know them today, the answer is easy: they are not responsible; they are the last of their race, restricted in geographical distribution, restricted in numbers, and struggling for their very existence.

To some this may seem like too positive a statement; but if it should be challenged, we should ask, "To what could the cycads have given rise?" The only possibilities are the Cordaitales, Ginkgoales, Coniferales, Gnetales, and the Angiosperms.

The Cordaitales, as the ancestral stock of the Coniferophyte line, might be expected to show resemblances, if any were to be found; but in habit they are very different from the Cycadophytes. They are the forest types, while the Cycadophytes bore somewhat the same relation to them that the ferns of today bear to the forests in which they occur. The leaves are prevaillingly simple, contrasting sharply with the prevailing pinnate or twice pinnate leaves of the Cycadophytes. Not enough is known of spore-producing members in the Cordaitales, to make safe comparisons, but the Cordaitales certainly had well-developed cones; so that, in this feature, they had progressed far beyond the Cycadofilicales. The fact that the cones were compound, while those developed later in the Cycadophyte line were simple, would indicate that the Cordaitales were from a different stock. We believe the available evidence indicates that the Cordaitales have come directly from the Pteridophytes; but whether they have come from the fern section or from the lycopod section is a problem in the solution of which morphological characters of still undetermined value are balanced against each other.

In the Ginkgoales, the pollen-tube structures, with the two motile sperms, present a startling resemblance to the corresponding structures in the cycads, even to the blepharoplasts developing into spiral ciliated bands, the peculiar behavior of the persistent prothallial cell, and the haustorial habit of the pollen tube. The extensive free nuclear period in the development of an embryo with two cotyledons is common to the cycads and Ginkgo; but here the resemblance ceases. The plant body and the strobili make relationship seem impossible. As far as the Mesozoic cycads are known, they afford no better Ginkgo resemblances.

In my opinion the Bennettitales are no more nearly related, although I once tried to compare the long-stalked ovules of Ginkgo with the ovulate strobilus of the Cycadeoidea type.

Even if we go back to the Paleozoic Cycadofilicales, it seems no easier to establish a relationship. Besides, the Ginkgoales can be accounted for quite naturally as an offshoot from ancient Cordaitales stock.

A relationship with any of the Coniferales would be even more difficult to establish. Corresponding structures are too contradictory. The large pinnate leaves of the Cycadophyte line do not compare well with the small, entire leaves of the Coniferophytes; nor does the unbranched trunk of the former compare well with the profusely branched trunk of the pines and Ginkgo.

In trying to provide progeny for the Cycadophytes, some have cast a hopeful eye upon the Gnetales, because the staminate flower of *Welwitschia* has a sterile ovule and thus presents a bisporangiate condition in which a vivid imagination might see some resemblance to the bisporangiate strobili of the Bennettitales. But my imagination is too weak to see more than a superficial resemblance, even in this feature; while a comparison of the stems of the two phyla, the comparison of pinnate leaves with simple leaves, and of simple strobili with compound strobili, seems impossible.

Could the Cycadophytes have given rise to the Angiosperms?

For the living cycads, we should answer with a positive *no*. This conclusion cannot be escaped, if we compare the haustorial pollen tube and its contents with the sperm-carrying pollen tube of the Angiosperms. The large, ciliated, highly differentiated sperms of the cycads are headed for extinction rather than for evolution into the comparatively simple structures of the Angiosperms. The extensive free nuclear period in the development of the cycad embryo does not compare well with the total lack of such a period in the Angiosperms. However, reductions in the free nuclear period are not entirely impossible.

It is true that the general habit of the cycad, with its unbranched stem and crown of pinnate leaves which form an armor of leaf bases, is so strongly suggestive of palms that the layman calls *Encephalartos* the "Bread palm," *Dioon* the "Dolores palm," *Cycas* the "Sago palm," etc. But the resemblance is superficial. A section of the palm stem shows an advanced monocotyl condition, and the flower is truly monocotyl. It may seem like begging the question to say that the Monocotyls have come from the Dicotyls, but we believe this has been proved as definitely as anything is likely to be proved in relationships.

The resemblance between the Bennettitales and the Angiosperms is about the same; but here an attempt has been made to reconcile the floral structures. The resemblance pointed out was between the Bennettitales flower and a sympetalous flower. Our objection here would be along the same line: the sympetalous condition is a modification of the polypetalous, and the Sympetalae, like the Monocots, have come from the Archichlamydeae.

In the Cycadofilicales we are nearer the source of things, but the discrepancies keep becoming greater and greater and indicate that we are on the wrong trail. Like the hasty student, trying to pigeon-hole *Eryngium yuccaefolium* among the Monocots, we need to go back and make a fresh start.

We have tried to show that the Cycadophytes have come from the ferns, by way of the Cycadofilicales directly or as an early branch from the Bennettitales; and we have also tried to show that they have not given rise to any other seed plants.

This might seem like a logical place to stop, for we have tried to answer

of two questions: "What was the origin of the cycads?" and "Have the cycads left any progeny?"

But it would emphasize the answer to the second question if we could show that the visible progeny could be referred to some other ancestry. In case of murder, the victim constitutes a concrete fact to be accounted for. The defendant may claim he didn't do it; but it adds weight to his claim if he can cast suspicion on some one else.

So let us ask another question: "Could some other group have given rise to the Coniferophytes and the Angiosperms"? We shall consider the two groups separately.

If the Coniferophytes have not come from Cycadophytes, they must have come from the ferns or from the lycopods. This is a problem, in the discussion of which leaf gaps are balanced against leaves, pinnate leaves against simple leaves, and abaxial sporangia against adaxial. I believe the evidence is sufficient to establish a Pteridophyte origin; but the comparative claims of ferns and lycopods do not appear the same to me as they did several years ago.

As far as the seed is concerned, some of the Paleozoic lycopods, like some of their living descendants, had progressed so far that their megasporangia are separated from seeds by arbitrary definitions rather than by facts.

We separate the Gymnosperms from the Angiosperms by the ovules on open carpels and ovules enclosed in an ovary; and the distinction is good and very useful in a taxonomic key; but rigid definitions may harden our ideas and may prevent us from getting an unbiased view of the facts.

In most Angiosperms, except epigynous forms, the ovules appear on open carpels, the closed ovary developing later. In cases like the Ranunculaceae, the integuments of the ovule appear and the embryo sac is well started while the carpel is just as open as in any Gymnosperm. In the Amentiferae, the ovules are well started before the carpels close; and in Podophyllum, sometimes the carpels do not close at all, the ovules being borne on perfectly open carpels, as in the Gymnosperms.

In considering this whole subject, we must remember that the extinct forms which have been preserved are mostly woody, especially in the Mesozoic. Has there been an extensive herbaceous flora which has disappeared? Have we lost herbaceous Gymnosperms which may have given rise to herbaceous Angiosperms? And could such herbaceous Angiosperms have given rise to the woody Angiosperms which became prominent in the Cretaceous?

Unless such an herbaceous flora has arisen and disappeared, it is necessary to derive the Cretaceous Angiosperms from woody forms; and this means from more or less well known Cycadophytes or Coniferophytes. Such attempts have been made. We have already paid some attention to the claims of the Cycadophyte line.

In looking for the origin of the Angiosperms, the claims of the Coniferales

and the Gnetales may be considered separately, although they have much in common.

Familiar representatives of the Coniferales show more resemblances and fewer contradictions. The plant body is similar, and the internal structure of the stem often shows striking resemblances. The catkins of the Amentiferae may not differ much, morphologically, from some of the cones of the Coniferales; the pollen-tube structures of Angiosperms could be derived from those of Coniferales, and the embryogeny could be reconciled. The leaves are harder to reconcile, but leaves are very susceptible to environment.

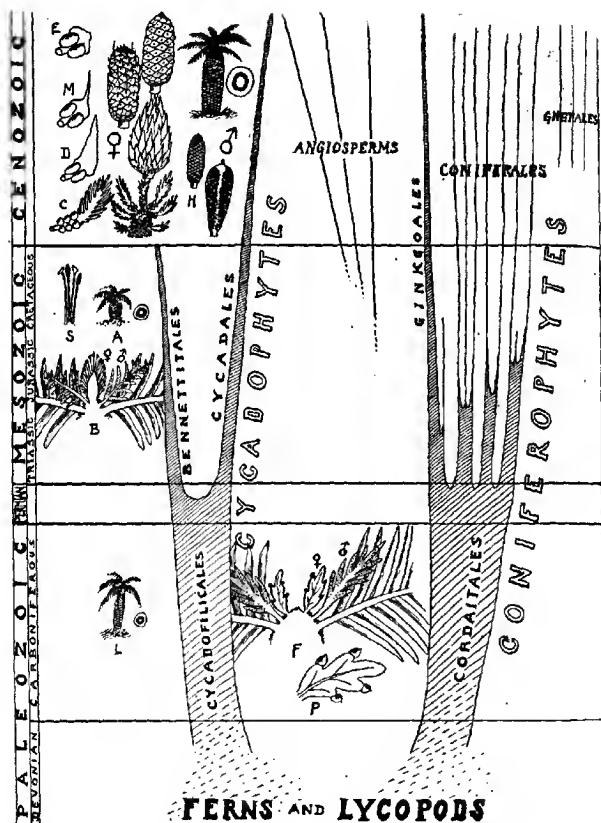
While these resemblances would not induce us to claim any Coniferales yet described as the ancestors of the Angiosperms, we believe they indicate the direction of the trail. We should remember that most of our Paleozoic and Mesozoic material is woody, and that there is a possibility—I believe there is a strong probability—that a great herbaceous vegetation has failed to be preserved, or, at least, has not yet been discovered. In such an herbaceous vegetation, leading up to woody forms, I believe the missing links will be secured, and that the Angiosperms will be found to extend much farther back than any available records have indicated.

The Gnetales show some striking Angiosperm characters. Most botanists, looking at the habit and leaves of *Gnetum Gnemon*, would call it a Dicot, and the histology of the stem continues the Dicot impression. In *Ephedra*, the habit, the strobili, and the spermatogenesis show Angiosperm features. It is so evident that the leaves have been reduced from more pretentious structures, that they need not constitute any objection.

In this connection, the less said about the leaves and habit of *Welwitschia*, the better; but its flowers, especially the staminate flower with its sterile ovule, would pass for Angiosperm flowers. The only objection seems to be that definition relating to open and closed carpels. Fortunately we have reached a stage in botanical development at which definitions need not interfere with research; for we do not put the Liliaceous *Agapanthus* in the Dicots simply because it has two cotyledons; or *Nelumbo* into the Monocots because it has only one cotyledon. So the open and closed carpel need not be absolute marks separating all Gymnosperms from all Angiosperms, and the presence of one condition or the other need not interfere with research into the origin of the Angiosperms.

It is easy to be humorous and to say that an ancestor must be older than the offspring, and that, therefore, the Gnetales, with no geological record, could not qualify as progenitors of anything. But here, again, we must remember the possibility, or probability, of an extinct herbaceous flora, which, very late in its history, developed a few woody members. Earlier in its history, it may have given rise to herbaceous Gnetales and to primitive Angiosperms, which developed into the woody forms of the Cretaceous.

We have tried to show that the Cycadophytes have come from the ferns and that they have not left any progeny, outside of the Cycadophyte line:



CHAMBERLAIN: CYCADS AND THE PHYLOGENY OF SEED PLANTS.

and we have tried to emphasize the second claim by showing that the Coniferophytes and Angiosperms—the undoubted progeny of something—can be referred to another ancestry.

EXPLANATION OF PLATE VI

Diagram illustrating some features of the Cycadophytes and Coniferophytes.

At the bottom: *L*, a diagrammatic representation of a member of the Cycadofilicales, with a transverse section of the stem at the right; *F*, an idealistic view of spore-producing members; *P*, pinnule of *Pecopteris* with seeds on the margin.

In the middle: *A*, habit of one of the Bennettitales with section of stem; *B*, bisporangiate strobilus; *S*, two seeds on long stalks and two scales.

At the top: habit of a living cycad; *C*, sporophyll of *Cycas* with crown of sporophylls at the right; *D*, *Dioon*; *M*, *Macrozamia*; *E*, *Encephalartos*; each with corresponding cones at right; *H*, male cone with a single sporophyll below. All very diagrammatic.

DISTRIBUTION AND RELATIONSHIPS OF THE CYCADEIDS¹

G. R. WIELAND

I. DISTRIBUTION

Plant geography is an impressive subject. It should find extension in time. Hitherto, little more than the fossil plant localities have been indicated. But the larger outlines of the Mesozoic forests must yet appear. The characteristic forms are slowly being determined; and sufficient progress has been made in paleogeography to permit initial hypothetical mapping of some of the forests. That even this rougher mapping discloses new facts is certain. With the old continental boundaries in view it becomes logical to ask why the Rhaetic plants of the Virginia-North Carolina coal field are so megaphyllous, while those of the southern Andine region are very microphyllous. Does not a larger part of the Jurassic Ginkgo record also indicate wide climatic variation, second only in extent to that of the time of the Glossopteris flora? Would it not be singular if plant evidence remained wholly at variance from that of the insects and invertebrates, indicating climatic cooling in the late Trias and early Jura, not local in character?

When one-sided evidence is once recognized as such, it becomes less misleading. The picture of the typical Mesozoic forest with a tropic sun beating on its xerophylls has been too grandly simple. A remnant of the equisetes, ferns, Araucarias, cycads, the pines, and the Ginkgos! Think this over. No real forests except coniferous "pure stands" from the close of the Permian to the Comanchean angiosperms? Unbelievable. The evidence already carries us much further, and the fact is being slowly disclosed that varied forests of microphyllous cycadeoids must have had a greater area than all other gymnospermous forests put together, all through Triassic and Jurassic time.

The record is not scanty, as I know from the field. There has been no reason for the view that the fossil cycads are simply the underbrush of tropical forests, or were merely columnar-stemmed fringing types like the palmetto. Yet this has been the only view. Nathorst, indeed, left open the question of the habitus of *Wielandiella*; but Jeffrey thought this form was procumbent. *Williamsoniella* (see fig. 1) would look less so. There is, however, no evidence for procumbency in either case. On the contrary, the branching in both these small-stemmed cycadeoids is but little simpler than that of some magnolias, and it is easier far to look upon them as shrubs,

¹ Invitation address read before the joint session of Section G, A. A. A. S., the Botanical Society of America, and the American Phytopathological Society, in the symposium on the "Phylogeny of Seed Plants," at St. Louis, December 30, 1919.

or as trees with a habitus not unlike some of the araucarians, the Brazil pine for instance. The point is all but proven, despite the fact that the actual histologic structure awaits fortunate discovery. By any fair analogy the pith must be little or no more developed than in young magnolia shoots, or in cone-bearing branches of araucarians; while the wood structure could not have been very different from the cycadeoidean type. Furthermore,

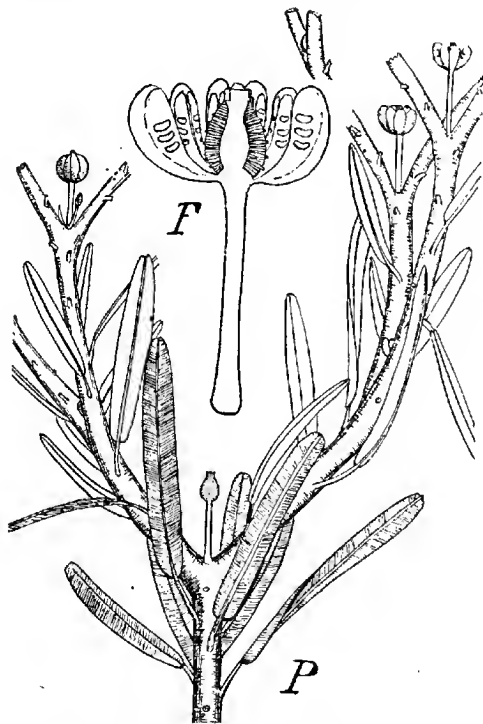


FIG. 1. *Williamsoniella coronata*, from the mid-estuarine series of the mid-Jurassic of the Yorkshire coast (at Gristhorpe). From the restoration of Hamshaw-Thomas. *P*, branch-end with flower-buds; *F*, a single flower enlarged twice. The central cone of the flower is surrounded by a whorl of synangia-bearing scales.

along with the small branches go small leaves, and the small perfect flowers, just as suggestive of forest types as those of the tulip tree. Evidence fails

for the view that the fertile dichotomizing branch ends, all thus far found, are anything else than the broken-off branches of trees. Just such branches of conifers of like or of older age are found. The chances that these forms had either structures or a habitus in any way indicating procumbency are exceedingly small. In groups or in forests they might have had some likeness to screw pines of mountainous rather than of tropic rain forest districts. The peculiar Pandanus forest of the Lokon of the Celebes is here suggested. But the point to note first is, that there is the fullest reason to believe that the small Tacnipteroid leaves of the small-flowered cycadeoids are related to innumerable megaphyllous types of truly tropic habitat, only the latter would be less plastic forest elements.

Whether this view of relative aplasticity for these megaphylls is right or wrong, they soon undergo extinction, after in their prime vividly recalling in both habitat and habitus the earlier coal-swamp floras. Neither *Williamsoniella* nor *Wielandiella* taken by itself indicates tropic plants at all. They were probably tropophylls or plants which shed their leaves with the seasons. The stems are usually found bare, the attachment of the dissociated leaves being determined only with difficulty. These are in a word generalized plants which so far as habitus goes might well grow in temperate to cool climates. Until far more is learned about them they should at least be held valueless as indices of tropic climates. But as the small-stemmed cycadeoids were related to the contemporaneous Ginkgos, and at the same time to early angiosperms, the inference becomes direct that either they or their close relatives already had the capacity to live in every clime.

There is also a suspicion that study of the associated ferns may compel revision of the long-accepted view of the universality of tropic climates throughout the Mesozoic. A. G. Nathorst, the most eminent living student of fossil plants, says of these suggestions in a letter just received: "I think you are quite right that during the time when the Ginkgophytes and Cycadophytes dominated, many of them must have adapted themselves for living in cold climates also. Of this I have not the least doubt. Remember, for instance, *Juniperus communis*. If *Juniperus* were extinct, and conclusions were drawn from all the other species found fossil in the parallels where they now live, it would be believed that the whole genus was bound to live only in the temperate climates. Yet *Juniperus communis* thrives well in Greenland."

Since current opinions of Mesozoic climates as based on plants are so open to challenge, any details which can possibly be learned about the cycadeoid distribution have a doubly important bearing on phylogeny. But it must be freely admitted that the subject can only be approached slowly, and is here considered superficially.

In a fossil form distribution is, to use a long and emphatic word, bi-dimensional. Distribution in a living form is simply lateral; but in fossils it is both lateral and vertical with more or less uncertainty at all limits.

As a rule, more is known of the vertical range or persistence in geologic time than can possibly be learned of the lateral range for a given period. And in nearly all fossils the probable period of extinction is more determinable than the first appearance. This follows for several citable reasons, and especially in the case of plants. Nearly everything, moreover, depends on the habitus of the plant, and upon where it grew. Generally the three thousand species of coal plants appear cosmopolitan because in the Carboniferous certain coastal plains were peculiarly favorable places for conservation, and now the economic value of coal so abundantly laid down leads to vast excavation over hundreds of square miles of the rocky strata, and through thousands of feet in thickness. How different is the case where some Permian, Rhaetic, or mid-Triassic horizon is studied. The excavation for material then depends on the enthusiasm of about a dozen men, taking the world over. This explains almost in a word why the record in the Carboniferous seems extensive, and in later periods much scantier.

It has long been held that cycads or Cycadophytes, as now more broadly named, dominated the Jurassic especially. But probably botanists, who have outnumbered paleobotanists a hundred to one, have generally been taken aback on noting that the score or more of well-marked post-Carboniferous floras seldom include more than 100 species in all. And on comparing, for instance, the Liassic of Scandinavia, England, India, and Mexico, it is even more disquieting to find that the species look stereotyped, as if they belonged to a few nearly related groups and gave but a vague picture of contemporaneous vegetation. But here the graver difficulties end. Except in the case of the Mesozoic gymnosperm stems, vast in quantity, of rare beauty of conservation, and urgently demanding study, the paleobotanist quite invariably deals with larger features. Just as the microscope reveals histologic detail, so separation in time magnifies structural and other changes to the point of visibility.

Thus far there appears to be no great fallacy in taking the cycadeoids from a generalized point of view and by percentages observing their ratio of abundance to the other forms of the successive horizons. This is in effect a rough consensus of plant life taken from age to age. The results are of course open to different interpretations, and it is most difficult to draw lines between all of the greater groups. In going back there is a gradual mergence of Coniferophyte, Cycadophyte, and Ginkgophyte foliage toward the seed-bearing quasi-ferns, at once indeterminate and startling to observe. Then very far toward the early Paleozoic there seems to be some kind of contact between the early seed ferns, and the older Lepidophyte types, also leading toward the primitive gymnosperms. As to whether, well down in the Devonian, some of the Lepidophytes of the *Pseudobornia* alliance were in near contact with *Archeopteris*, and like the later seed ferns also led into the primitive Coniferophytes, is the real sphinx riddle of paleobotany—far more so than the origin of the angiosperms. It looks

as if plant life would have been best balanced in the phytologic sense if the Devonian Pteridophytes and Lepidophytes both sent their quota into the gymnosperm complex. In that case some Cordaites (?), araucarians, and perhaps some other Coniferophytes would be these Lepidophyte derivatives.

Cycadales.-

Persistent, dioecious,
unisexual strobiles
of increased size.

Hemicyadales:-

I. Specialized.
often bisexual,
extinct.

II. Generalized and
mainly micro-florous
[Relatively extinct]

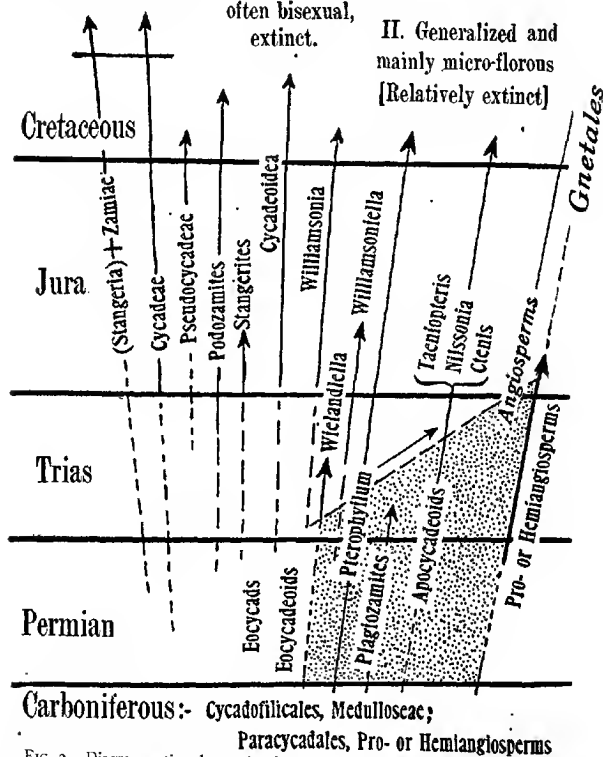


FIG. 2. Diagrammatic scheme showing the position in geologic time of primitive and hypothetical groups related to the cycads and cycadeoids, and their assumed relation to the basal angiosperm types. The position of the latter is indicated by the stippled area.

bearing in mind, then, these greatest of all problems of plant history, many of the genera so difficult to place could be cited. A few may suffice. *Perotaxamites* lies on the cycadeoid-conifer boundary. *Brachyphyllum* stems most approach in structure as well as in appearance the cycadeoid stem types. But yet, by constant and consistent attention to main phases of the fossil plant alignment, and by continual revision of the percentual record of occurrence, the general nature of the forward movement of cycadeous plants can undoubtedly be brought out. It is very interesting indeed to find that in the Australian Rhaetic and Lias the proportions of the several plant phyla are in harmony with those noted elsewhere. In fact, there are certain features of Mesozoic vegetation which stand out as very important, and which could not be discerned without the aid of this percentual method. It displays the great abundance of the *Pterophyllums* at the earlier end of the cycadeoid record. Also, the *Taeniopteris* which are separated from the other forms by A. B. Walkom in his Australian studies, as they should be, are a singularly prevalent type in the late Triassic. They are often small-leaved, and if largely cycadeoid they are of course the forms which stood very close to the leaf types leading toward the dogbanes, the oleanders, and the Magnolias. In the Lias, where climatic variation is suspected, the stereotyped pinnate fronds of the tropics (Oaxaca) mark the culmination of plants apparently cycadeoid.

As an example of distribution and relative abundance expressed percentually, the subjoined table (table 1) from Walkom may be scanned. It displays the relations found in the plants of the "Ipswich series" of the lower Mesozoic rocks of Queensland, Australia.

TABLE 1.

	No. of Species	%	%	%
Equisetales.....	5	15	15	15
Filicales.....	10	30		39
Filicales (<i>incertae sedis</i>).....	3	9	57	
Taeniopteris.....	6	18		24
Cycadophyta.....	2	6	6	
Ginkgoales.....	7	21	21	21
Total.....	33			

Such tables are certainly helpful, with the fossils actually in hand. And their graphic value can scarcely be denied. As Walkom observes, "they must be used with a good deal of caution, lest they lead to quite incorrect and even absurd results; although with a full realization of their value and also their drawbacks, they may yield interesting and to some extent reliable results." Note that the *Equisetales* suggest a Triassic abundance, while the considerable number of *Filicales*, with a large (early) gymnosperm series, is in accord. The general description of the flora given by Walkom sustains his conclusion that these plants may be of upper Triassic (or

Keuper) age. But in the original list there are four species of Thinnidiales, which are probably ginkgoid, and if so considered would reduce the Finales to a more normal proportion. Further tabulations of Mesozoic plants may be found in Volume 2 of my "American Fossil Cycads."

As in the case of the Dinosaurs, the cycadeoids after they reach relatively high specialization, move rapidly toward extinction during the phase of continental development which begins with the great epeiric seas of the upper Cretaceous submergence and ends in the full continental areas of the glacial stages and later or present arid climates. This is the period, not of angiosperm origins, but of angiosperm dispersal and specific modification with disappearance also of the early or transition angiosperms.

One other observation, and the subject of distribution may be left aside, it hardly being practicable to go into moot questions of generic distribution for the moment. In almost all instances the doubtful border of cycadeoid foliage ends in a tree forest of seed ferns, Cordaites, pines, Araucarias, and Ginkgos, but never in recognizable scrub. With the legitimate inferences from stem structure, and the characters of Wielandiella, and especially of Williamsoniella in mind, a much greater Mesozoic forest comes into view. Nothing in paleobotany appears more probable now than that amongst the cycadeoids will be found the lost forests and the greatest forest makers of the Mesozoic.

II. RELATIONSHIPS

If the systematist can recognize a degree of relationship or similarity between the monocot arums and screw pines, and the Ranalean dicots why is not oblique or unequal convergence the more difficult explanation? Those resemblances must have been still greater in the Jurassic forest. But even then these several lines must have been distinct. Nothing has so limited progress in phylogeny as the *palting* of "paleontologic trees." If more attention were given to the elementary facts of the record as found progress in its interpretation would be surer. For whether, in that lofty mood, variation is held to be epigenetic, or orthogenetic, or whether it be held that there is less of continuity and that the main course of biologic change goes on in select lines and types with much outright extinction, both the object and the method of phylogenetic study remains the same. The primal object is to determine the order in which structures and organs appear, and thus to find how the groups of animals and plants are related in time. From any more philosophic viewpoint classifications are only made to serve this purpose, and thus afford a sound basis for the more ultimate study of variation. And therefore, while classification is at every stage in the development of plant study a serious task, classifications themselves should be viewed as wholly impermanent. As a definition of classification, then, may be given, simply, *present views of relationship*.

In attempting to elucidate some of the principles which must influence

our views of the relationships of the cycadeoids, and in assembling the broader known facts and passing on to some quite legitimate inferences, the present object is of course to bring into view mainly those features which have a bearing on the phylogeny of seed plants in general. In the glimpse just had of distribution, attention was mainly fixed on relationships within the Cycadophytes. It was found that no headway could be made in picturing the real extent of cycadeous vegetation in the Mesozoic, without some consideration of the hypothetical variation within the group. And that subject could have been pursued much further. Now it is the aim to single out analogies without the group. Being essentially gymnosperms, it will be contended that the cycadeoids relate themselves to the other spermatophytes in the following order of closeness: firstly to the cycads, secondly to the seed-bearing quasi-ferns, thirdly to the Cordaites and Dolerophyllum, fourthly to the Ginkgophytes, fifthly to Araucaria, sixthly to the Abietineans, seventhly to the magnolias and other dicotyls, and eighthly to the Gnetales. This order may be conveniently followed in discussion.

The Cycads

There has been a wide divergence of opinion as to whether the cycadeoids are in any near sense related to the cycads at all. But as knowledge of the existent and extinct groups has been extended, and as better defined terms have been reached, the difference of opinion or of viewpoint is lessened. So distinctly is this true that it would hardly be fair to name any one, either in this country or in Europe, as holding unqualified views. One might say that the likenesses between the two groups are distinct and the differences striking, or the reverse. And this alternative or disposition of some to lay stress on vegetative features in this classification, and of others to emphasize fructification, has found expression in the division of the super-group Cycadophyta into the Cycadales and the Hemicycadales or half-cycads. Certainly no one would deny that the cycads and cycadeoids are the two most contiguous of the greater gymnosperm phyla. The two groups must have come from the same section of the Carboniferous plant alignment. Throughout all of Permian and Triassic time they must have been in close histologic contact, and by lower Jurassic time about all the visible difference in the wood was the preponderance of scalariform wood in the cycadeoids in contrast to the pitted wood of the present-day cycads. Both wood types occur in both groups, and histologists are welcome to think as they please about which is the more primitive. Of course, while insisting upon points of vegetative resemblance it is the large pith and thin woody cylinder of the petrified stems, or the family Cycadeoideae, which is cited. But the fact cannot be too strongly emphasized that such stems are of unusual type. They are the only ones definitely known amongst the cycads. It was seen, however, that the characteristic and plastic cycadeoids were no doubt small-stemmed and microphyllous. The single strand leaf trace

appears rather primitive as compared with the double strand of the cycads, and may have had some relation to microphylls and plasticity of type. But the double strand appears in ancient gymnosperms; and, also, in Ginkgo the leaf traces arise from the stele as a pair of collateral bundles. Nor would it be cause for surprise to find in some small-leaved cycadeoid with a thin cortex such a double trace, or even two weak lateral traces.

Turning to fructification, the contrast between the two types is great because of sporophyll emplacement coupled with retention of the primitive microsporophyll in one instance and a carpophyll in the other. But the cycadeoid microsporophyll was also plastic and reduced in well attested instances from both the Triassic and Jurassic rocks. It might, therefore, be believed that some members of the original cycadeoid alliance had both the mega- and microsporophylls reduced in spiral emplacement. Such, however, would lead toward Gnetalean or coniferous types, and what appears to have been an instance will presently be cited. It may be added that the observation that the Cycadeoidea microsporophyll was as distinctly horned or bicornute as that of the Mexican *Ceratozamia*, and freely tomentose, brings the groups together a bit, and at the same time suggests possible form variation toward conifers.

The Seed Ferns

Derivation of the Cycadophyta in totality from ferns is in accord with the views held by botanists throughout all the studies of existent and fossil plants for the past two or three score years. This is a section of botanical science to which its votaries may point with confidence if not with pride; and further discoveries are awaited with the certainty that they will be made. The seed fern *Lyginopteris* was fully hypothesized before its final discovery. But adequately to treat this antecedent relationship would require an attention to structural details beyond the limits of the present discussion. It is safe to say that both the vegetative and the reproductive hiatus between the quasi-ferns and the early cycadeoids is bridged by known structures, found isolated to be sure, though conclusive. One of my colleagues has also given consideration to this fundamental relationship.

The Cordaites and Dolerophyllum

The origin of the Cordaites is so lost in geologic antiquity that an otherwise rather striking affinity is more or less obscured. It must be remembered, too, that in going back so far toward the beginnings of these plants with seeds often of enormous size, the likenesses must frequently be the merest of parallelisms. Could sessions like ours have been held about the close of the Devonian, when *Callixylon Oweni* flourished where we now stand, it may well be imagined that discussion would have turned on whether the Cordaites seed was phyletically related to the synchronous ancestral cycadeoid seed or not.

The singular *Dolerophyllum* is another type very difficult to place, but with a seed fern antecedent in *Pecopteris* (fig. 3). The linear spirally inserted leaves are not unlike those of the *Cordaites*. The large pollen believed to pertain to these leaves is borne on a large, fleshy, peltate disc

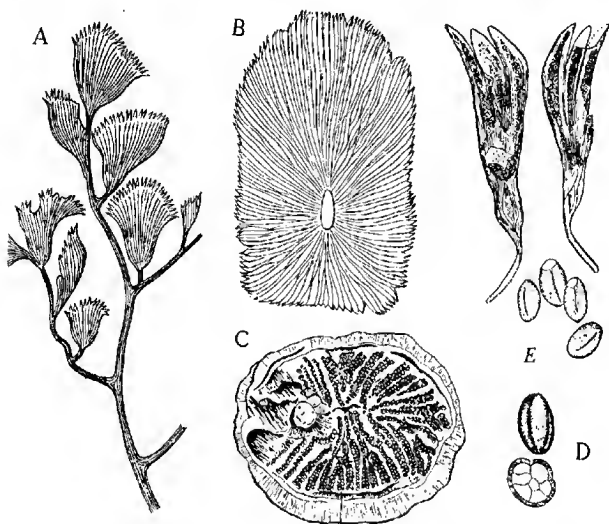


FIG. 3. Ancient staminate disks: *A*, *Potoniea adiantiformis* of the French Carboniferous, a Neuropterid bearing staminate cups (natural size); *B*, *Linopteris antiqwa*, also of the French Carboniferous, showing under side of disk (several times enlarged); *C*, *Dolerophyllum*, a fleshy staminate cup (with pollen enlarged at *D*); *E*, *Codonotheca caduca*, showing the microspores (enlarged), and the toothed and symmetric campanula (natural size) from the Carboniferous of Mazon Creek, Illinois. *A* and *B* from Bertrand, *C* and *D* from Renault (Seward), *E* from Sellards.

Note. The microspores of *Ceratozamia* are 40 microns long, those of *Cycadeoidea* 50 to 100, of *Stephanospermum* 120, of *Codonotheca* 300, and those of *Dolerophyllum* 400 microns long. All the evidence thus far tends to indicate that ancient microspores were large.

6 by 5 cm. in a series of very elongate pockets more or less regularly radiating from the eccentric insertion. Whether these pockets are rows of more or less confluent sori or synangia is not clear, but possible, since vascular strands run between them. If the disc were symmetrical, or could it be shown to arise from fusion in a whorl of fertile leaflets, affinity to the staminate discs of *Gnetum* and the cycadeoids would be foreshadowed. Somewhat similar discs are seen in the Neuropterids called *Potoniea* and *Linopteris*, also in

Neuropteris Carpentieri of Hirston. The completely symmetrical disc Codonotheca, an abundant and striking fossil in the coal measure nodules of Mazon Creek, Illinois,² also appears to fall within this Neuropterid-Dolerophyllum alliance. It is believable that the study of these ancient discs must eventually show the manner of evolution of the large vascular gymnosperm seeds; unless indeed the synangial hypothesis of Professor Margaret J. Benson for the origin of seeds accounts for the sole method.

With this brief mention Dolerophyllum may for the present be dismissed. As a floral type it finds place somewhere amongst the Medullosans, an immense assemblage of Paleozoic stems structurally antecedent to those of the Mesozoic and later Cycadophyta. Unfortunately, fructification in this group, though not entirely hypothetical, is about the blackest *incognita* of paleobotany.

The Ginkgos

A great Ginkgophyte phylum, falling but little later in geologic time, next arrests attention. The Ginkgos are mainly Permo-Jurassic, and

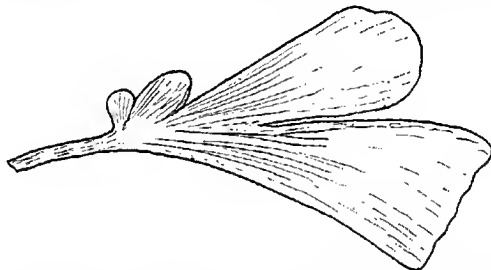


FIG. 4. *Rhipidopsis*, a ginkgoid leaf which occurs in the Permian of India and Russia, and which strongly suggests relationship to the South American fronds mentioned in the text as typical in the Rhaetic. Only the outline is shown. This remarkable foliage type was described by Schmalhausen, and a photograph showing the typical Ginkgo venation is given by Seward in his "Fossil Plants," volume 4. Here only half the natural size.

especially exemplify the fact that the forward movement in plant evolution was always widespread; with the higher of the extinct forms of the successive periods always holding near to the persisting mean. Specialization in the Ginkgos seems to rise little beyond oddity of outer feature. Berry mentions as members of this phylum, Ginkgophyllum, Saportea, Whittleseyia, Trichopitys, Dicranophyllum, Rhipidopsis (cf. fig. 4), Psymphyllum, Gomphostrobus, Tricophyllum, Feildenia, Phoenicopsis. There are also the handsome leaves called Baiera, with the staminate flowers, or Antho-

² On the split surface of a Mazon Creek nodule of my own, no larger than the palm of the hand, four complete Codonotheca discs appear, and there are parts of a fifth and sixth. They seem to have split off regularly, like fronds.

is, possibly known. Some of the foliage no doubt falls near or within the Medullosans. But other forms may be added. Of such the lax cone of *Williamsonia* with two-seeded megasporophylls denotes variation toward the cycadeoids, so distinctly contemporaneous in the Trias-Jura transition of Rhaetic time. Here also I would mention the two remarkable Y-shaped frond types known as *Dicroidium* and *Thinnfeldia*, both recently shown by Antevy to be xerophytic. They have been referred at one time to another to several gymnosperm groups, but not hitherto to the Ginkgos. In any case the fernlike aspect relates these frond genera on the seed-fern side. Nor do they appear remote from that somewhat more cycadeoid leaf type called *Ptilozamites*. This genus and the palpably ginkgoid and varied *Baiera* foliage, occur in well marked association in the Rhaetic of the southern hemisphere. No one who studies the Rhaetic and the succeeding Liasic or lower Jurassic plants in the field will ever again rest under any doubt about a steady and well marked transition from seed fern foliage toward cycadeoid and ginkgoid foliage. With this point emphasized it may be permissible to omit closer reference to structure, and to ask attention to a cycadeoid relationship of a more recondite character because of a certain lack in the accumulation of fossil evidence, namely that to *Araucaria*.

Araucaria

That the araucarians attained specialization early, with retention of much primitiveness of feature, and that they are a discrete line coming down from the old cycadofilicalean complex, is indicated by analogy to the cycadeoids. It is now evident that *Araucaria* has more in common with cycads and cycadeoids than was earlier supposed. The robust armored stem is analogous to that of the cycadeoids, this being true of structure, of cortical development, and of both the primary and the secondary branching. The roots freely send up young plants, and the seedlings are stout, cycad-like, and remarkably tenacious of life. Renewed growth of the reproductive shoot from a lateral bud is cycadaceous and cycadeoid, comparison being made with *Wielandiella* and *Williamsonia scotica*. The large pith and thin woody cylinder of the shoots, vegetative and reproductive, and the complete transition from foliage to fertile scales of the large cones are also cycad-like, as well as still more decidedly cycadeoid. The megasporophyll with its small ligule finds a counterpart in the decurved microsporophyll of the cycadeoids, and is aplosporophyllous, with the seed imbedded.

Nor is it necessary to regard the araucarian seed-cone as greatly different from that of Cycadeoidea merely because the seed is decurved like that of cycads, instead of erect. In reality the fertile sporophyll is surrounded by infertile members almost identically as in Cycadeoidea. This significant comparison has been hitherto overlooked. Moreover the araucarian microsporophyll is also decurved and at the same time sends up an acuminate scale-tip which may well be regarded as the analogue of the spur seen in the

cycadeoid microsporophyll. In fact, if the latter is reduced, as it may be, and then imagined to be spirally inserted as in forms already hypothesized, the main features of the araucarian staminate cone appear to view. Finally, the presence of a leaf gap opposite the outgoing foliar trace in the stem and seedling adds still more weight to this far-reaching comparison. The double and multiple traces do not of course compare directly with the single trace of the known cycadeoids, but with cordaiteans or cycadeans. But some or all of the resemblances or parallelisms pointed out must have been more marked in the Jura. The araucarians have probably simplified more or less since then, in accord with their simple foliage type and narrowing distribution.

Pines, and Gymnosperm Stem Structure

Amongst gymnosperms the pines of today are of course the type remotest from the cycadeoids; but so far as may be judged from the lax or less compacted, even leafy, types of gymnosperm cones which prevail in the late Paleozoic and early Mesozoic, there may be hypothesized a marked similarity between some of the ancestral pines and the cycadeoids. This general subject is a most difficult one, and adequate study of the abundant gymnosperm stems in most fresh-water deposits of the globe from the Paleozoic down has never been made. Obviously such work can be pursued only by the most expert students of wood structure. Enough has been done, however, to lead to the belief that tracheidal change has followed some fixed trend, just as has floral change.

Bailey and Tupper have examined the size variation in tracheary elements of the secondary wood of vascular cryptogams, gymnosperms, and angiosperms. It is positive that there has been much decrease in tracheidal lengths since the evolution of the upper Devonian Cordaite forest, and in widely separated groups. Also, Willis and DeVries have observed a tendency of plants to present certain features and groupings or segregations, which persist or fail over wide areas. There is a tendency to division into "locals" and "wides" which leads to a belief in some ratio of age to area. The theory alone is in a sense self-destructive. If changes in secondary wood are progressive through the ages, and if in the more superficial characters of leaf and flower the vegetation of forest and plain is still subject to simultaneous change, there is no such thing as *age* and *area*. One form is about as old as another. But right or wrong, the contributions cited taken in combination with the work of Clements on "plant succession," form the chief current contribution by botanists to the broader study of evolutionary theory.³

³ Digressing a bit: Such coordinated change went on amongst the wonderfully patterned ammonites all over the globe all through the Jurassic. And why not? R. A. Harper says: "From the one-celled alga or fungus to the highest plant or animal, the differentiation of nucleus, cytoplasm, chromosomes, spindle fibers, etc., is everywhere present; and in their general nature and functions and in their interrelations, these structures are the same.

The general subject of later tracheidal¹ structures as bearing on the origin of modern stem types is too broad to take up in any detail. But a few observations may be made. There are a number of facts accessible especially in the great work of Solereder, going to show that no one process can account for the origin of vessels. Possibly they have at times arisen by direct evolution very anciently in unknown and upland Arctic floras, and later secondarily from both pitted and scalariform tracheids. Perhaps, as Jeffrey contends, scalariform wood can even result mainly from pit fusion. But it will not do to call only pitted wood ancient, and the scalariform types the more modern. The remarkable Carboniferous *Lyginopteris* has the large-celled, many-pitted wood, but either the contemporaneous relatives or the ancestral types of the quasi-ferns may and must have had the scalariform wood. The peduncular wood of cycads and cycadeoids alike is scalariform.

This much may be safely said: In the pines a high degree of ray specialization is geologically recent. Also in the dicotyls the course of ray change must be coordinated with recent development of storage tissues. Such structures may be subtracted in order to glimpse or to hypothesize antecedent dicotyl wood in the Jurassic. If then the pit wood of *Drimys* and *Trochodendron* with its suppressed growth rings, and the scalariform wood of *Trochodendron* and *Tetracentron*, have any significance at all, the inescapable conclusion is that both cycadeoid and cycad wood is old and near the type basal to many modern forms. It is indeed delusive to read this history in terms of *Gnetum* alone.

Dicotyls and Gnetaleans

Analogies, rather than relationships, between the cycadeoids and the dicotyls and gnetaleans may be quite conveniently discussed as under a single topic. For here the gymnosperm border line is crossed, and all the near relationships cease. The older view of dicotyl derivation through early conifers and gnetaleans is now opposed to the newer view of near cycadeoid derivation, in part coupled with suggestions of an extreme parallelism amongst both gymnosperms and angiosperms. But following various recent and thorough studies of the gnetaleans, the idea that they indicate the real angiosperm precursors is even accentuated by some. Lignier and Tison say the gnetaleans are merely aberrant angiosperms which retain early gymnosperm features and lead toward the amentifers. And Hallier even suggests they are reduced dicotyls like *Loranthus* and the *Myxodendraceae*.

E. W. Berry is the most recent to follow and emphasize the Lignier and Tison view, so far as relates to descent. He says that the primitiveness of

... Evolution has not consisted in the production of new types of protoplasmic structure or cellular organization, but in the development of constantly greater specialization and division of labor between larger and larger groups of cells."

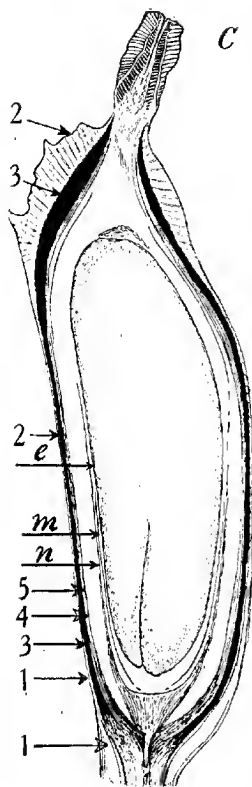


FIG. 5. *Cycadeoidea Dartoni* seed in longitudinal section (radial to cone). 1, 1, termination of tubular celled cortex forming supporting basal cup to erect seed; 2, 2, the blow-off layer of radially set cells enveloping shoulder region much as in *Gnetum Gnemon*; 3, 3, lateral and shoulder development of the radially celled stony layer which is prominently four- or five-ribbed; 4, a thinner sclerenchyma of small elongate cells or fibrous hypoderm; 5, main inner parenchymatous layer; *n*, the nucellus arising from the chalazal base containing central supply of numerous small scalariform tracheids; *m*, megaspore membrane; *e*, dicotyledonous and exalbuminous embryo filling the nucellar cavity. Length of seed four millimeters.

C

the magnolia flowers is illusory, and he finds reasons for dicotyl derivation from the Gnetales in: (1) the inflorescence, (2) floral morphology, (3) the details of sporogenesis, (4) fertilization, (5) embryogeny, (6) organization of vessels in the wood, (7) broad rays, (8) companion cells in the bast, (9) habit and foliage, and (10) the dicotyledonous embryo.

This is a sweeping summation, so regardless of plant history that it would scarcely be expected to come from a paleobotanist. It does not set aside the possibility that the gnetaleans have merely paralleled the angiosperms, as Seward and others have suggested. In any sense of finality in evidence, the validity of these points falls one by one. It will not do to compare the gnetaleans of today with the cycadeoids of the Trias. And what the gnetaleans were like in the Jura, the fertile time of angiosperm origin, is too uncertain. Neither can 20,000 to 30,000 species be safely hypothesized for them as in the case of the cycadeoids. They can not be hypothesized out of hand on vague leaf characters. Commenting, then, *seriatim* on these "points": It must be insisted that taking the greatly reduced *Wielandiella* flower of the Trias, nothing is simpler than to infer related forms with few-seeded flowers grouped spirally. It is a mistake to attach all significance to this mere sporophyll emplacement, or to relation between singly borne and inflorescent flowers. This might arise late or early. Next, it is wrong from even the purely histologic standpoint to assume that the *Gnetum* flower of the Jurassic was more reduced than cycadeoid flowers. Besides, though sepa-

by such a great lapse of time, the *Gnetum* and cycadeoid seeds show the peculiar resemblances pointed out by Emily M. Berridge and Mrs. T. Day (see fig. 5). As Seward well says, it would be "rash" to hold such resemblances without phylogenetic significance. So also the details of sporogenesis may merely tend to parallel those of angiosperms, and may thus be deceptive—illusory, as Berry thinks the primitiveness of the magnoliaceous flower to be. Nor is it necessary to assume that none of the cycadeoids advanced beyond a motile antherozoid stage. This view I was quite the first to put forward strongly, and must retract. The negative view alone is permissible as a hypothesis.⁴

In the embryogeny is perhaps found the very strongest evidence for dicotyl derivation from gnetaleans. W. P. Thompson observes much similarity, and, some differences which may yet prove fundamental; but the subject is discussed by one of my colleagues.

So far as regards the gnetalean wood, it must be urged once more that the vessels have been held to have peculiarities, and that the extent of parallel development since the Jurassic cannot yet be fairly estimated. W. P. Thompson says the vessels "should be removed from all discussions of the angiosperms." If so; then, similarly, the rays. The foliage of *Gnetum Gnetum* is of a peculiar netted type with a striking fineness of mesh not so very dissimilar from that of the laurel-leaf magnolia. Netting, however, probably developed progressively in the seed plants, and could as readily accentuate in pinnate cycadeoid blades, either primitively or secondarily netted. If the net is primitive in *Gnetum*, it can be primitive in the cycadeoids. If it resulted from separation, or alternant elision of the pinnate veins, with invasion of the marginal net in an earlier *Gnetum*, leading towards oleanders and magnolias, the same development could go on in cycadeoids. There, too, a real basal form is recognized in the fern-like *Taeniopteris* leaves of the flower-bearing *Williamsoniella*. That net venation was very anciently and widely present in the Cycadophytes is indicated by the fern-like mesh in the pinnules of the Indian *Dietyozamites*, one of the stereotyped Liassic cycadeoids.

To continue, W. P. Thompson, in concluding one of his studies of gnetaleans, quotes an abbreviated statement of Scott on the "claim" of a cycadeoid-angiosperm ancestry as resting simply on three points—strobilar organization, fruit-enclosed seeds, and the exalbuminous nature of these.

⁴ Stefanie Herzfeld emphasizes my own observation of conductive nucellar tissue in Cycadoidea as evidence of zooidogamic fertilization. And that this mode was formerly more or less widespread amongst the gymnosperms must be believed. Evidently, then, there is need to have a care in excluding such a mode from the cycadeoids. But it may be noted that the exact comparative study bearing on this point is scarcely made, while the object here is mainly to state the case theoretically. The zooidogamic type of fertilization must have disappeared mostly as the modern angiosperms arose, or mainly in the interim between the Rhaetic and the Cretaceous. So that in this time of great change amongst the cycadeoids as well it seems unlikely that they continued more primitive in this respect than conifers.

Then Thompson gets on to say that the negating cycadeoid features are the cycadean habit and leaves, motile spermatozoids (!), the primitive gymnosperm condition, and absence of angiosperm adumbration in the gametes, endosperm, or embryo. Thompson as a botanist pays even less attention to chronology in his assemblage of characters than does Berry as a paleobotanist. A cycadeous habit for *Williamsoniella* or *Wielandiella*! Never, if the thought is only of gnetaleans! And, of course, if fossil foliage is to be excluded from the reckoning, what should be done with *Tumboa*? Leaf variation is not a special feature of gnetaleans. Besides, as they still persist, they probably changed late or more or less inadaptively, and too slow to be ancestral to anything.

Those wishing to examine the gnetaleans from the critical phylogenetic point of view should begin with the work of Lignier and Tison. It is briefly excerpted and commented on in my "American Fossil Cycads," volume 2, pages 235-237. In their summary of the features of the hypothetical Gnetaloid precursor of the angiosperms may be discerned a fundamental type which could not have been remote from some of the contemporaneous cycadeoids. The great question remains, at what period did the main separation actually begin? When this becomes even approximately known, intensive search may be made for the fossil evidence and field relations.

If allowed a subscription of faith, if permitted a prediction, then I make mine that future work will develop the fact that plant evolution has followed an orderly sequence and course. Its current has been as sure, as steady, as that of the majestic river by the banks of which we stand. From age to age the great groups have come down side by side, some specializing certain features a little more, others holding to more generalized structures, or losing apparent relationships because of reductions, but all undergoing that endless change from which neither genus nor species has ever been exempt. Almost no forms, scarcely a family, need be regarded as more ancient or more modern than any other.

Huxley, with his keen insight, noted as a most astonishing thing the fact that, taking all animal life, the proportion of extinct ordinal types is so exceedingly small. In the 125 orders of animals only about ten percent, perhaps now fifteen percent, appeared wholly extinct. But with all the advances made in paleozoology revealing complexity of form, there has been much of simplification, and type after type has been found much older than at first thought.

The plant record is, so far as the higher types are concerned, both older and more fragmentary than is much of the animal record. Its study has been late in development, and has often lagged. The results from the different continents are as yet poorly coordinated. Nevertheless the broader outlines of ancient vegetation already appear. The known gymnosperms and the pseudo-gymnosperms or cycadeoids go back to the Paleozoic,

and it is conceivable that all the antecedent types of the angiosperms are equally discrete, always separate lines, leading back to the first forests that clothed the land in the Devonian. And throughout all later time it may well be believed that with the poles where they now are, and with that tremendous rhythmic diastrophism or emergence and subsidence of the continents, there was an ever-present plasticity in the plants of the arctic areas. But along with the theory of hardness and invasive power for the plants of the high north and far south would perforce go a similar potentiality in plateau and mountain vegetation.

EXPLANATION OF PLATE VII

Above: Apical view of *Cycadeoides dacotensis* (type) showing terminal helicond of young chaff, enveloped fronds, and scale leaves, with various fruit buds, about $\frac{1}{4}$ natural size.

Below: *Cycas revoluta* (left), showing cone about 15 inches high, and (right) the same in a younger stage of growth.

These figures illustrate extreme cycadophytan types.



WIELAND: THE CYCADEIDS.

